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Bioactivity, Production, and Energy Utilization of Lakes

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ABSTRACT

Unter Verzicht auf die verwirrende Vielzahl von ökologischen und anderen Seetypen können alle Gewässer der Erdoberfläche nach dem Umfang der organischen Produktion in ein System steigenden Trophiegrades eingeordnet werden. Oligo-, Meso-, Eu-, und Poly-Trophie bezeichnen den ungefähren Grössenbereich der Produktivität.

Nicht nur die Primärproduktion, sondern auch alle sekundären Produktionsstufen, einschliesslich der bakteriellen, charakterisieren den Trophiegrad der Gewässer. Daher wird die Bioaktivität des Biosystems, die diesen gesamten Komplex der organischen Umsetzungen umfassen soll, als Grundlage für den produktionsbiologischen Vergleich der Gewässer angesehen. Die Bioaktivität schliesst in sich die Bildung potentieller Energie sowohl die Rückführung derselben in kinetische.

Der Umfang der Primärproduktion und die Menge der biogen ausnutzbaren organischen Substanzen allochthoner Herkunft werden mit Hilfe der Kohlendioxyd-Akkumulation des Hypolimnions bestimmt. Die Primärproduktion ist nicht immer von der mittleren Tiefe der Seebecken abhängig. Produktionstiefe und Produktionsdichte beeinflussen sich gegenseitig entscheidend.

Der Kohlenstoffgehalt des rezenten Sedimentes ist aus der Grösse der anaeroben Kohlendioxydbildung ableitbar. In den untersuchten Seen Norddeutschlands ist das Verhältnis der gesamten potentiellen Energie zu ihrem ungenutzt bleibenden Anteil, d.h. der Grad der Ausnutzung potentieller Energie, stets direkt proportional der mittleren Tiefe.

Der als organische Substanz je Oberflächeneinheit des Schlammareals abgelagerte Energierest ist proportional der gesamten potentiellen Energie je Volumeneinheit des ganzen Sees.

Auf Grund der beschriebenen Gesetzmässigkeiten, die das Leben in Gewässern beherrschen, ist ihre Bioaktivität in Gramm Kohlenstoff je Quadratmeter des Oberflächenareals je Zeiteinheit zu bestimmen aus den Grössen der Primärproduktion und der Energieausnutzung, die sich unmittelbar aus der mittleren Tiefe der Gewässerbeckens ableitet.

During the 35 years since Thienemann and Naumann proposed the first division of lakes into oligotrophic and eutrophic types, many additional lake types have been described. Originally the quantity of organisms produced served as the basis for this classification, but later, and particularly by Naumann himself, ecological factors were also employed for characterizing the waters.

Consequently, both the cause and the result of organic production have become so closely associated in respect to the terminology of lake types that it has become difficult to compare different lakes. But this comparison must be an essential goal of limnological research if we are not to be content merely with a pure description of the conditions occurring in lakes. If, for example, we compare the properties of a subarctic lake with those of a tropical one, it is apparent that temperature exerts a decisive influence on the biogenic metabolism, even when the nutrient contents of the waters are essentially the same. We find that cold-loving or warm-loving organisms occur as characteristic representatives of the biotas of these respective lakes. These and other facts about the lakes, important as

they are in themselves, do not enable a direct comparison of the two waters, but rather elucidate only the controlling factors or the particular pathway of biogenic activity. Similar difficulties arise in the comparison of soft waters with hard waters, or of lakes with a low or high salt content, respectively. Just recently Damas (1956) has described the problems involved in the trophic classification of tropical lakes of Ruanda-Urundi in Africa. Although these waters have a rather small standing crop they have a sharp oxygen depletion in the hypolimnion and a gyttja-like mud rich in diatom shells. Thus oligotrophic and eutrophic characteristics are associated in tropical lakes as was first described 25 years ago from the lakes of Indonesia by Hummel, Ruttner, and Thienemann.

PRODUCTIVITY AND BIOACTIVITY OF BIOSYSTEMS

Because of the difficulties that arise in a study of the typology of waters it appears desirable to use the intensity of organic production as a basis of comparison, rather than the factors influencing it, and thus to return to the original concept stated by the founders of the trophic system. According to this concept, all surface waters regardless of their size and of their ecological characteristics can be arranged in a continuous series of increasing trophic level (Ohle 1955). Hence, the terms oligotrophy and eutrophy, as well as mesotrophy and polytrophy, designate only the approximate magnitude of productivity. A natural separation of these trophic levels from one another does not exist because they intergrade imperceptibly. They can be recognized only by placing arbitrary limits on them. It is interesting that Birge and Juday as early as 1932 expressed the following criticism of the large number of lake types already proposed by that time: ". . . it is doubtful whether a separation into more than two general types has any particular value."

The trophic level of a body of water is a function of its overall productivity. The question is, what do we mean by this? We recognize the various productions of phytoplankton, zooplankton, bottom fauna, submerged aquatics, fish, and so forth. But we must consider not only the primary production of plant substance and its secondary utilization by animals, but also the mineralization processes, for these also lead to organic production, namely of bacteria. Instructive examples of this have been described by Kriss (1954) from the Black Sea. Kalle (1948) and Macfadyen (1950) have defined the production rate of a sea region as the quantity of organic substance produced per unit time through the utilization of solar energy. At the same time the authors point out that the polar sea understandably is nearly 10 times richer in living organisms than tropical oceans. The divergent temperatures of the sea regions concerned are responsible for these differences in standing crop, which therefore cannot indicate the production rate. However, the uptake of solar energy by the planktonic organisms likewise does not furnish a complete picture of the life processes occurring in the water masses, if the metabolic activity of the organisms is not considered at the same time.

We have to consider the decomposition and respiration processes. Just as in the oceans, there are lakes that have the same magnitude of organic production in their epilimnion but show great differences in the extent of the mineralization occurring in their lower as well as in their upper layers. All these biogenic transformations of organic matter belong in the concept of trophic levels. Grim (1950) has chosen the term "Umsatz" (turnover) for the metabolic rotation of inorganic components through all kinds of organic compounds back again to the mineralized stage. Elster (1954) has proposed replacing the term "Umsatz" by "Umlauf" (circulation).

Starting with the well-known definition given by Thienemann (1931) for productivity, I have included all mineralization and respiration processes as well and have related the concept to units of volume or surface and time in the following manner (Ohle 1955): the specific productivity of a biotope is the quantity of organisms and their excreta produced autochthonously per unit time and per unit volume or surface area, and also the intensity of its mineralization.

In order to avoid any confusion that

might result from combining the concepts of standing crop, of primary production, and of all secondary production rates, we prefer to consider the energy cycle rather than the quantities of organic matter involved in the various life processes.

Furthermore even the term productivity is ambiguous since it has been used by various authors in quite a different sense (cf. Kalle 1948, and Macfadyen 1950). Therefore, the present author proposes that the term productivity be replaced by *bioactivity*. The following short definition may be given for the bioactivity that characterizes bodies of water, small ponds or great lakes as well as streams and the oceans:

The specific bioactivity of a biosystem is its capacity for the formation of potential energy and the subsequent reconversion of this into kinetic energy per unit time and per unit volume or surface area.

This definition, which encompasses the complex dynamics of life processes occurring in waters, is related to the concept of Feninger's "limnodynamics" (1950) and Macfadyen's "metabolic activity" (1950) or Elster's "metabolic dynamics" (1954). The term "metabolic activity" first was used by Bornebusch (1930) for the interpretation of his research on the fauna of forest soils. Lindeman (1942) working with Hutchinson clearly distinguishes productivity as a rate (e.g. cal/cm^2/year) from the efficiency of the productivity as a ratio, i.e. a dimensionless number. The expression *production* should be reserved exclusively for the various components of bioactivity, which in itself represents such an involved complex of processes concerned with the uptake and release of energy that it might never be completely unravelled, since it includes the entire dynamics of life processes.

Such a definition may seem too complicated. One might desire to have bioactivity more narrowly defined so that its value could be determined analytically over its full range. However, it is obvious that the different organic transformations are very closely interrelated and hence difficult to study individually. Our biological, chemical, and physical methods enable us to understand only parts of the entire metabolism. These at times can be characteristic of the overall bioactivity and can serve as indicators of it, although in many instances the magnitude of a particular branch of production does not bear such a direct relationship to the overall dynamics of biogenic metabolism. In other words, at times certain methods might be particularly useful, yielding reproducible results, and yet not be applicable at all in other situations.

Understandably such a rigorous standard must also be applied in the interpretation of chemical analyses. The opinion quite widely held even today that the trophic level of a body of water can be ascertained simply by determining its nutrient concentrations is justified only in isolated instances, because all the other ecological factors, such as temperature, light penetration, water movement, antibiotics, etc., are important in influencing organic production. In contrast to this, Faegri (1954) has proposed defining trophic level as quality of the water (not of the lake), and recently Findenegg (1955a and 1955b) arguing along the same direction concluded that trophic level (Trophie) or nutrient content of the water should be distinguished from its production.

On the other hand, chemical data can lead to success when they are used to calculate the balance of biogenic metabolism. It is well known that limnology experienced a rapid development through the inauguration of oxygen deficit calculations by Thienemann, and later on by Hutchinson (1938) and many others. Phosphate and other inorganic components have been used in the same manner as oxygen.

DETERMINATION AND CALCULATION OF CARBON DIOXIDE ACCUMULATING IN TROPHOLYTIC LAYERS

Building on the knowledge obtained by estimation of the hypolimnetic oxygen deficit, the biogenic cycles of carbon have been investigated with reference to the problems of bioactivity in waters (Ohle 1952). The following is a short description of the procedure used for this purpose.

Carbon dioxide understandably represents the most important initial and final com-

ponent of the biogenic metabolic reactions. As a result of the photosynthesis carried on by chlorophyll-containing plants and certain bacteria, the carbon of the carbon dioxide utilized becomes the bearer of potential energy. Although the latter represents only a very small portion of the incoming kinetic solar energy, it is the driving force of the entire metabolism of a body of water, which continually utilizes this supply of potential energy. In so doing there is again produced kinetic energy, almost exclusively in the form of heat. Lakes that experience a stratification of their water masses in summer, chiefly as a result of temperature differences between surface and bottom, become differentiated into an upper trophogenic and a lower tropholytic layer. On the basis of the chemical changes occurring within a certain period of time in the tropholytic deep-water zone, into which the biogenic remains of the trophogenic zone settle, and especially on the basis of the ensuing enrichment of the deep water, it is possible to draw conclusions about the amount of epilimnetic production. Even when no permanent summer stratification into epilimnion and hypolimnion is developed, it is still possible and profitable to calculate the metabolism from the carbon dioxide accumulating during periods of temporary stratification. The only situations to which this method cannot be applied are those in which the water undergoes complete and unremitting circulation.

It must be emphasized further that at the present time we do not have an adequate understanding of the magnitude of the short-term carbon cycle or so-called "short circuit cycle" occurring in the epilimnion, that is, we do not know how often in a given period of time a particular carbon atom is incorporated into organic matter and again released as carbon dioxide before it has finally settled down into the hypolimnion (or metalimnion) in the form of organic detritus. Our present information indicates that these epilimnetic transformations do not proceed in all waters at the same rate. Obviously temperature exerts a decisive influence on these processes and especially on respiration. In tropical waters a small biomass may exist in spite of a high level of bioactivity. Further understanding of these problems probably will be furnished by use of the C^{14}-technique (Steemann Nielsen 1952, 1954) and the light-and-dark-bottle oxygen method (Riley *et al.* 1949). The results of Ryther (1954) suggesting that in their respiration plankton algae can utilize to a considerable extent the organic compounds newly formed by photosynthesis is of very great interest. From our investigations along these lines the tentative conclusion can be drawn that in the epilimnion of north-German lakes in summer carbon is utilized three times on the average before it is withdrawn from the metabolism of the trophogenic zone.

For the calculation of the CO_2-accumulation it is necessary to determine the hypolimnetic concentrations of oxygen, carbon dioxide, bicarbonate, and ammonium, as well as temperature, at as many different water depths as possible in the lake being investigated. These analyses should be made at short time intervals over a period of time preferably of at least one month's duration, if stratification persists this long. Adjusting for the known volumes of the individual depth strata of the lake, the total carbon dioxide that has accumulated during this time interval is then calculated. In this procedure the following principles are to be taken into consideration:

Only half of the increase in the bicarbonate content can be ascribed to the current metabolic cyle of the lake, since the balance originated from the carbonate supplies in the mud and got into the water in a purely allochthonous manner. On the other hand, the formation of ammonium carbonate depends upon completely new mineralization of organic substances, and its entire amount must therefore be considered. From the observed decline in oxygen content the quantity of carbon dioxide formed by aerobic oxidation of organic matter is calculated, although not on an equimolar basis, but rather by means of the conversion factor 0.85. This is the mean value for the respiratory quotient of aquatic organisms. After subtraction of this value of

aerobically produced CO_2 from the total amount present, the remainder must be doubled, since on the average under anaerobic conditions only half of the organic carbon participating in the fermentation processes is mineralized to CO_2 (Ohle 1952).

In this manner the accumulation in the entire hypolimnion within a given period of time is determined. By dividing this quantity of carbon dioxide by the volume of the epilimnion and relating this to a convenient unit of time, preferably a month, one obtains a CO_2-value in ppm, which is to be trebled on account of the short-circuit carbon cycle. The value is designated as the "relative assimilation intensity". The word "relative" has been chosen in order to emphasize that the values serve to characterize the assimilation intensity only within certain limits. That must be so when we consider how incompletely we understand the extent of the short-circuit carbon cycle, as well as the magnitude of exchange between epilimnion and hypolimnion.

EVALUATION OF PRIMARY PRODUCTION BY ESTIMATION OF CARBON DIOXIDE AND OXYGEN

The results obtained for a number of north-German lakes by use of the method described are illustrated in Figure 1. In these and neighboring waters Thienemann discovered 35 years ago the narrow relation existing between the oxygen deficit and the morphometric features of the lake basin. More recent investigations have verified this conclusion again and again. Indeed, the oxygen deficit expressed as ppm O_2 per unit time in the hypolimnion bears a narrow inverse relation to the mean depth of these eutrophic lakes, as is evident in Figure 1. However, the rate of autotrophic production is not at all reflected by the shape of the oxygen stratification curve, since it is influenced by the special morphometric features of the lake basins, as has been well known since Strøm's first communication (1931) on the subject. His arguments have been supported by many other authors. We can draw conclusions about lake productivity from the oxygen deficit of the

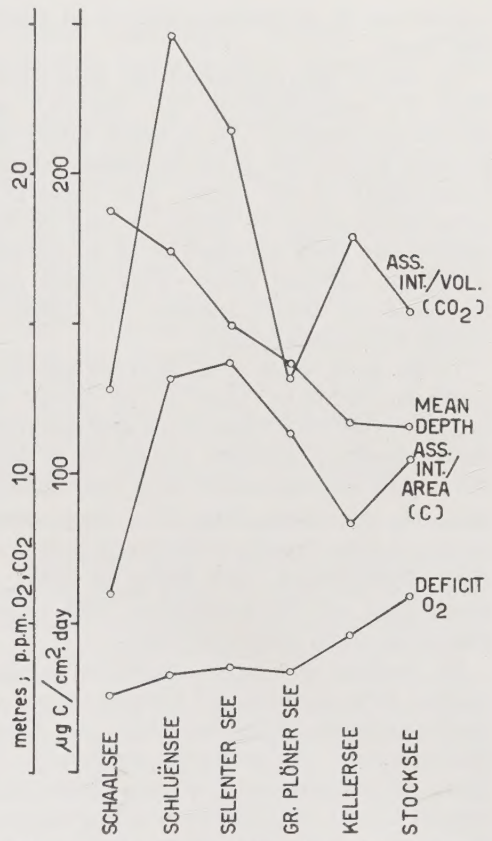

FIG. 1. The oxygen deficit (ppm/liter of hypolimnion/month), assimilation intensity (ppm CO_2/liter of epilimnion/month, and μg C/cm^2 surface/day) for 6 north-German lakes arranged in order of decreasing mean depth.

hypolimnion by computing the value per unit area of the upper surface of the hypolimnion (Hutchinson 1938) or by referring to the epilimnion per unit volume and unit time (Ohle 1952). In this way we obtain values for the production of the trophogenic layer in ppm O_2 or C, respectively.

However, since the hypolimnion of strongly eutrophic lakes does not contain a sufficient store of oxygen necessary for the aerobic oxidation of the organic substances that are furnished to it from the epilimnion, the oxygen deficit is representative of autotrophic production only in oligotrophic or weakly eutrophic water. On the other hand, the accumulation of carbon dioxide is not limited in the hypolimnion because it is produced there. For this reason the carbon dioxide accumulation is suitable for the

estimation of production rates in all stratified lakes.

By use of this method it has been found that the magnitude of the "relative assimilation intensity", or in other words the primary production, is not dependent on the mean depth of the lakes. But there is a close relationship to depth as long as the deep water does not lose all of its oxygen supply in summer time. This result corresponds to that obtained by Rawson (1955) in Canadian lakes.

In the good series of lakes investigated in northern Germany there is no linear relationship between mean depth and assimilation intensity, referred either to a unit volume of the epilimnion or a unit surface area of the lakes (Fig. 1). Deep lakes having a large supply of dissolved oxygen in their hypolimnion can have as great a production of phytoplankton and other plants as much shallower lakes.

In shallow waters we expect a higher trophic level because of a greater supply of plant nutrients furnished from the mud. Nevertheless, the primary production of these waters does not increase, either with respect to unit surface area or unit volume of the lakes. Evidently in the shallow lakes investigated the greater *production density* is compensated for by a smaller *production depth*. This means that the production density will be limited by lack of nutrients or biocoenotic factors within the dense population, at the same time as the production depth is decreased by lack of light, a major part of which is absorbed by planktonic organisms and detritus in the upper water strata. Thus, changes in production density and production depth are closely correlated. This result seems to be essential in view of the distinction and separation of water fertility (expressed by the biomass per unit volume) from the plankton production per unit surface area of tropical lakes (Ruttner 1952, and Thienemann 1954). Similar evidence is obtained in an entirely different manner by following the content of protein in the epilimnion, determined quantitatively by means of the biuret reaction (Krey 1952). Granted that the organic production predominating during the summer months does not necessarily characterize the annual production, nevertheless one can assume that waters are comparable with another at the time of their main bioactivity.

CRITICAL CONSIDERATION OF THE USE OF CO_2-ACCUMULATION FOR PRODUCTION MEASUREMENTS

We shall now consider several questions that are raised in the application of the carbon dioxide accumulation to calculations of production biology. As already explained, the method can be applied only where stratification persists for a sufficient period of time. Nevertheless, it has also proved valid in many ice-covered lakes, in spite of the difficulty there of recognizing a sharp distinction between the tropholytic and trophogenic layers. The magnitude of water exchange between epilimnion and hypolimnion, which even during the period of summer stagnation in lakes is brought about by wind-induced partial circulations, naturally reduces the quantity of the accumulated carbon dioxide and partially replenishes the oxygen store of the hypolimnion, thereby leading to a negative error in the calculated amount of production. By means of continuous observations on such waters the magnitude of this exchange can be determined and the necessary corrections can then be applied to the calculation.

In many lakes the mineralization processes are confined primarily to the upper part of the hypolimnion, bringing about in this region a so-called metalimnetic (or thermoclinal) oxygen minimum. In spite of this compression of the zone of mineralization, it is still possible to relate its accumulation of carbon dioxide to the magnitude of epilimnetic production occurring during a period of calm weather persisting for a week or longer.

In the case of a so-called metalimnetic oxygen maximum, such as can be brought about either by the photosynthetic activity of algae or by purely physical circumstances, the mineralization occurring in this stratum cannot be investigated any easier than in the epilimnion.

A further problem arises from the possible participation of older sediments in the

hypolimnetic accumulation of carbon dioxide. It is known that at a depth of a couple centimeters in the mud bacterial action continues, although weakly. As a consequence, the quantity of carbon dioxide accumulating in the hypolimnion must be somewhat greater than the corresponding quantity of organic matter produced in the epilimnion in the same interval of time. Nevertheless, on the basis of laboratory experiments and also direct investigations of lakes in summer and winter, it has been determined that the decomposition of older sediments does not introduce a significant error in the present procedure. Even when the temperature remains approximately the same, the fermentation of the surface mud sets in with unusual intensity at those times when dead algae are sedimented in greater quantities upon the bottom. By comparison, the decomposition of organic substances in the older sediments proceeds very sluggishly. It is possible that the positive error arising in this manner is largely balanced by the negative error resulting from the exchange of water masses across the metalimnion.

Finally, the allochthonous importation of organic substances might be regarded as a disturbing factor in the evaluation of CO_2-accumulation for determining the trophic level of a body of water. Humic substances and other organic materials can lead to intensive bacterial activity. The carbon dioxide originating in this way bears no relation to the autotrophic production of the lake, but is derived rather from the photosynthesis carried on by swamp, bog, and land plants growing in the drainage basin.

From another point of view, however, both the aerobic and anaerobic decomposition of allochthonous organic matter, i.e. its partial or total utilization by the biosystem, represent a part of lake bioactivity. In humic waters this source of energy is extremely important, because copepods and other organisms feed either directly on the organic particles or else on the bacteria adhering to them in great quantities. In reality there is thus no occasion to exclude the mineralization of allochthonous organic substances from the concept of autochthonous bioactivity. Rather it seems completely logical to have bioactivity refer to the entire biotic metabolism—to all types of autotrophic and heterotrophic functions. From this point of view, therefore, there is no principal difference between autotrophic and paratrophic development of limnic organisms in relation to bioactivity. Secondary productions, including that of bacteria, belong to the biotic dynamics. However, it must be remembered that in such humic waters, as for example those of Wisconsin, Michigan, Sweden, and Finland, no conclusions concerning the amount of primary production in the epilimnion can be drawn from the hypolimnetic CO_2-accumulation.

UTILIZATION OF POTENTIAL ENERGY BY LAKES

In order to obtain a further insight into the metabolism of lakes we shall now return to the closely investigated north-German clear-water lakes and consider the *anaerobic* formation of carbon dioxide. For this purpose we shall relate the portion of the accumulated carbon dioxide that has arisen anaerobically to the oxygen deficit. As Figure 2 shows, the lakes differ more strongly from one another in their values for anaerobic carbon dioxide

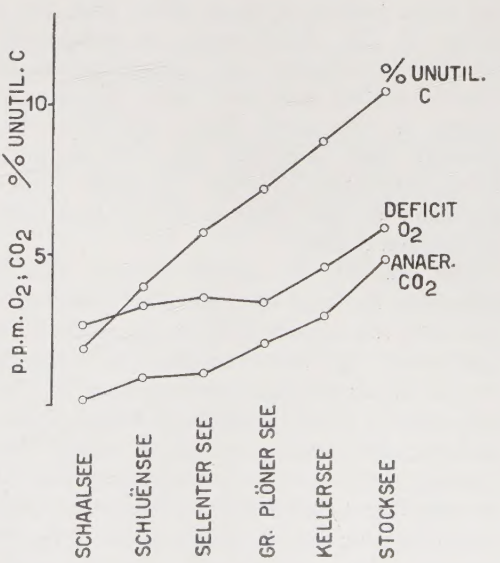

FIG. 2. Anaerobic carbon dioxide and oxygen deficit (ppm/liter of hypolimnion/month) and per cent of available energy (C) not utilized for 6 north-German lakes arranged in order of decreasing mean depth.

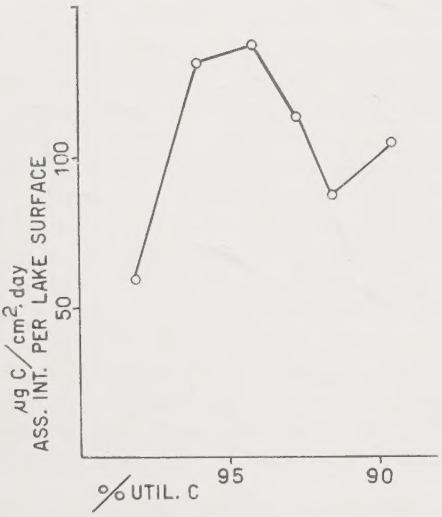

FIG. 3. Assimilation intensity (primary production, potential energy) expressed as µg carbon per cm² lake surface area per day, plotted against the percentage of the potential energy (C) utilized by the biota.

than in those for oxygen consumption. The deepest lake considered (Schaalsee) develops 0.2 ppm anaerobic CO_2 per month, whereas the shallowest lake develops approximately 25 times more than this. On the other hand, the oxygen deficits per month for the same bodies of water differ only by a factor of 2.3. This result is completely intelligible, because the mineralization of organic matter continues after the oxygen supply in the deep water has been exhausted, and therefore the CO_2-accumulation furnishes a more accurate representation of the biotic activity than does the oxygen deficit.

The quantity of carbon dioxide that is formed in the mud by anaerobic means and gets into the hypolimnion is approximately equivalent to the quantity of organic matter than remains permanently in the sediments. This conclusion is based on the well-founded results of physiological experiments that on the average only half of the participating carbon is oxidized under anaerobic conditions (Ohle 1952). If we compare the quantity of anaerobic CO_2 produced, or its equivalent content of carbon respectively, in the newly formed but permanent organic sediments with the total quantity of carbon dioxide accumulated, then we can calculate the utilization by the lake of the organic matter produced in the epilimnion, or in other words the energy utilization by the biota of the lake in per cent of the potential energy supply per unit of time. As Figure 2 shows, the lakes investigated present considerable differences. In Schaalsee only 1.8% of the potential energy remains unutilized, whereas in Stocksee 10.4% remains, indicating that deep lakes enjoy a much greater efficiency in utilizing potential energy than do shallower ones.

The magnitude of the actual organic production per unit volume of the epilimnion, on the other hand, does not show a consistent relationship to depth. Furthermore, no proportionality exists between the amount of available potential energy, or of primary production respectively, expressed as micrograms of carbon per square centimeter of lake surface per day, and the efficiency of the lake in utilizing this energy (Fig. 3). Independent of the quantity of potential energy available expressed as assimilation intensity, there occurs in the different bodies of water a weak or a strong transformation of the potential energy into kinetic energy as a result of the respiration of the organisms and the decomposition of their remains. From this it is apparent that the biogenic transformations and decomposition processes of the hypolimnion must be appreciated as important branches of the bioactivity of lakes, and their magnitude cannot be inferred from the amount of organic production in the epilimnion.

A further analysis of these investigations furnishes a still deeper insight into lake metabolism. Figure 4 shows that the efficiency of energy utilization in lakes is directly proportional to their mean depths. Thus morphometric features of lake basins have a decisive influence upon their rates of secondary production.

In spite of the fact that assimilation intensity or primary production is not always proportional to mean depth (Fig. 1), at least not in those waters that have a high trophic level, the intensity of conversion and destruction of organic substances is proportional to mean depth. Thus, a deep

lake which is poor in phytoplankton proves to have a rather strong respiration and mineralization activity at the same time, and conversely in shallow lakes these processes of conversion and destruction develop more sluggishly. In northern Germany oligogrophic or weakly eutrophic lakes having a mean depth of more than 20 meters mineralize up to 99% of the utilizable organic substances, whereas in eutrophic lakes, the mean depth of which is less than 10 meters, only about 85% of the available potential energy is utilized.

From this fact important conclusions can be drawn. First it is necessary to consider the changes that lakes undergo in their development over a considerable period of time. The continuous sedimentation of inorganic and organic materials brings about a progressive reduction of the mean depth of the lakes, so that the ratio between water volume and surface area continually decreases. In this manner the sediments exert an increasing influence upon the overlying stationary and circulating water. The water is provided in increasing degree with nutrients from the mud, and the higher level of nutrients can provide for an increased organic production. However, not only the morphometric features of the lake basins play a decisive role in this direction. From the time that a particular stage in the ontogenetic development of the water bodies is attained, namely as soon as the hypolimnetic water in contact with the mud suffers complete loss of its oxygen supply, there occurs an extreme change in lake metabolism. The increased yield of nutrients to the water from the mud, which under anaerobic conditions assumes immense proportions, is not always accompanied by a strong increase of autotrophic organisms. Indeed, the phytoplankton will develop luxuriantly in the upper water strata, but the production depth of the lake decreases inversely as the production density increases. Considering the epilimnion as a whole there can result even a decrease in the amount of primary production per unit volume as well as per unit surface area, as has already been discussed in detail. At least beginning with the complete exhaustion

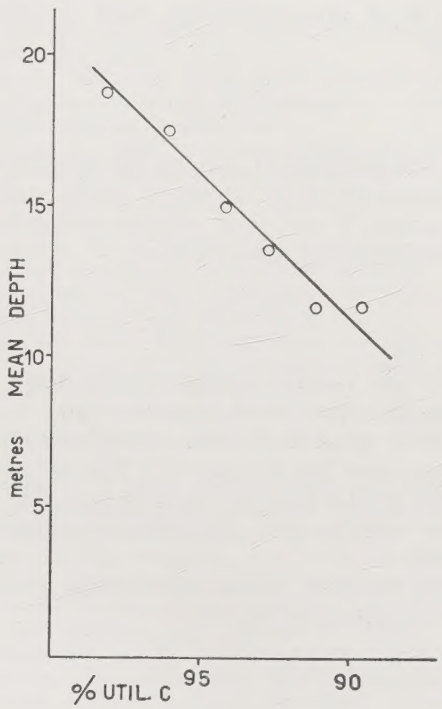

FIG. 4. Mean depths of the lakes, plotted against their efficiency of utilization of the available potential energy (expressed as per cent carbon).

of oxygen in the deepest part of the hypolimnion the intensity of primary production becomes independent of the shape of the lake basin.

In contrast to this, as the preceding investigations have demonstrated, the efficiency of energy utilization of the lake remains directly proportional to its mean depth, or conversely, the amount of potential energy eliminated from the lake expressed as a percentage of the total potential energy available remains inversely proportional to the mean depth.

Evidently the whole limnic dynamics of metabolism always depend very narrowly on the ratio between lake volume and surface area. This relationship can be formulated in simple mathematics as follows. If C_p is the total potential energy of a lake, C_s the portion of the total energy incorporated into the permanent sediments, D_m the mean depth of the lake, and z a

factor of proportionality, then it follows that

$$\frac{C_s}{C_p} = \frac{z}{D_m} \qquad (1)$$

In this equation D_m can be set equal to the quotient V/A in which A is the surface area and V the total volume of the lake. From this it is apparent that

$$\frac{C_s}{C_p} = z \cdot \frac{A}{V} \qquad (2)$$

It is now possible, without introducing too great an error, to set the surface area of the mud A_s equal to the lake area A, because by comparison the volume of a lake is such a much greater quantity than its area that the error introduced by this substitution is very small.

On the basis of this substitution the following equation derives:

$$\frac{C_s}{A_s} = z \cdot \frac{C_p}{V} \qquad (3)$$

This means that, neglecting the factor of proportionality z which is still to be determined, the unutilized potential energy (C_s) per unit surface area of mud is proportional to the total potential energy (C_p) per unit volume of the whole lake. Expressed in another way, the quantity of organic carbon sedimented per unit time per square meter of mud surface is proportional to the quantity of organic carbon that was present during the same time interval per cubic meter of the total lake. In other words, the quantity of organic sediment depends directly on the amount of organisms and other organic compounds distributed through the whole lake. The more diluted, so to speak, the organic substances are in the water mass the smaller is the percentage of them that will be sedimented. It is a remarkable fact that the thermocline does not effect this relationship.

ESTIMATION OF LAKE BIOACTIVITY

According to definition, the bioactivity of a biosystem consists of autochthonous primary production and all secondary productions based upon it as well as upon allochthonous organic substances. In order to estimate the total bioactivity of a lake it is necessary first to determine the available potential energy, i.e. the magnitude of primary production and the quantity of utilizable organic compounds furnished to the lake from its environment; and second, the efficiency of energy utilization. If, for example, the lake Schluensee in summer contains a potential energy, expressed as equivalent carbon of 39.6 g C/m²/month, and if the energy utilization of the body of water is 96.1% (38.1 g C), then its bioactivity, which is the sum of both the productive and destructive processes, is 39.6 + 38.1 = 77.7 g C/m²/month.

The greater the efficiency of energy utilization in a lake, the higher the intensity of life processes must be. These secondary productions certainly are ruled by van't Hoff's law, and therefore the factor of proportionality z which effects the relation existing between energy utilization and morphometric properties of the various lake basins will not have the same value under appreciably different climatic conditions. It is an urgent task of limnological research to prove this hypothesis and to clear up the real relationship.

As a matter of course, the way followed here is not the only approach to the elucidation of bioactivity. On the contrary, no link in the chain of organic production dynamics ought to be neglected by limnological research. The problems should be attacked from the most diverse biological, chemical, and physical viewpoint. Only then will it be possible to solve the difficulties which now prevent a complete understanding and explanation of the complex nature of bioactivity.

We cannot expect that nature, as complex as it is, can be squeezed into a simple scheme. The more comprehensive a system proposed as a working hypothesis is conceived, and the more all different points of view are taken into consideration, then the more likely will research lead to a deeper perception of nature. The results of investigations must be assembled stone by stone in order to achieve new understanding—leading to new problems.

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A Dynamic Height Method for the Determination of Currents in Deep Lakes[1]

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ABSTRACT

An adaptation of the oceanographer's dynamic height method to freshwater conditions, the method develops directly from the Smithsonian Tables of water density as a function of temperature and from Amagat's coefficients of compressibility. Pressure effects are handled by use of the decibar system. The calculated dynamic heights are plotted and contoured. Current directions are obtained by application of the geostrophic principle; current velocities are computed from the slopes of the surface topography. A table of specific volume anomalies, necessary for the height computation, has been developed. Sources of potential error are reviewed and assessed. The method has been applied to three synoptic surveys of Lake Huron, and the results obtained are both internally consistent and in good agreement with the behaviors of other parameters. When used with proper caution the method appears to be a promising technique for the study of certain circulation phenomena of large deep lakes.

INTRODUCTION

It is well known that freshwater is slightly compressed by pressure and expanded by temperatures above and below 4° Centigrade. For some decades the oceanographer has made use of similar phenomena to calculate current direction and velocity from density data, and from the reciprocal of density—specific volume. It appears that with certain modifications the oceanographer's dynamic height method of current determination can be applied to at least the deeper lakes.

The degree to which this application may be limited by the shallowness of lakes is not yet clear. The method depends upon the selection of a subsurface reference level at which currents are virtually absent. It is imperative that the reference level be below the depth of the turbulent mixing and return flow that result from wind action. It appears from the work of Mortimer (1951, 1954) that turbulent mixing and return may, under ordinary winds, attain two or three times the mean depth of the thermocline. The depth to which summer warming penetrates may also be used as a measure of the over-all depth of wind-caused mixing; the latter was used in Lake Huron (Table 3). On the basis of our present knowledge, the method appears to be applicable in lakes where the preponderance of depths is more than three times the mean depth to the thermocline.

It is strongly urged that currents determined by this method be checked against currents obtained by other means; lack of agreement may indicate that significant bottom currents are present and that bottom stress must be considered. The dynamic height method may be unsuccessful during periods of spring and fall turnover.

THE METHOD

The dynamic (or geopotential) height method deals with the calculated lengths of water columns which are considered to be standing upon the horizontal reference level. In each component segment of the water column at each station the resultant effect, on length, of compression due to hydrostatic pressure of overlying water and expansion due to temperatures above or below 4° C is determined. Summation of the resultant effects in all the component segments gives the column's length change resulting from the expansions and/or compressions of its parts. Addition of this

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length change to the theoretical length of the column under standard conditions gives the calculated height of the column top above the reference level under the prevailing conditions of pressure and temperature. The differing heights of the column tops at the various stations produce a "topography" of the water surface. From this dynamic or geopotential topography the current directions and velocities are obtained.

The freshwater method's primary length unit is the centimeter. Its use allows unusual convenience in operating with specific volume.

The effects of temperature on volume per unit mass have been obtained from the Smithsonian Tables as quoted in the *Handbook of Chemistry and Physics* (1949, Table of relative density and volume of water). The volume per unit mass is the specific volume.

$$\text{Volume/unit mass} = \text{specific volume} = a_{t,o} \text{ (at observed temperature and zero hydrostatic pressure)} \quad (1)$$

The coefficients of compressibility used are those of Amagat (1893)[2] as given in the *Handbook of Chemistry and Physics* (*op. cit.*, Table of compressibility of liquids). Amagat's coefficients for 1 to 25 atmospheres pressure at 0, 10, and 20° C were graphed, and the graph extrapolated to 30° C; from the graph the coefficient at each degree was obtained (Table 1).

Amagat's unit "contraction in unit volume per atmosphere" ($cm^3/cm^3/atm$) when multiplied by the number of volumes involved becomes compression per atmosphere (cm^3/atm); when one specific volume is used the compression is numerically the same as the coefficient and has the unit $cm^3/gm/atm$.

Since one atmosphere of hydrostatic pressure = 1 bar = 10 decibars = the hydrostatic pressure of ten meters of water, and one meter of water produces one decibar of pressure, the depth in meters is therefore essentially numerically equal to the pressure in decibars. Also

$$\text{Depth in meters}/10 = \text{atmospheres pressure} = p \quad (2)$$

Compression at observed temperature, C_t, (Table 1) multiplied by the *in situ* pressure at depth gives compression *in situ*

$$C_t \times p = \text{compression } in\ situ = \Delta a_{t,p}. \quad (3)$$

It is assumed that a lake has constant surface area during the short period when data are being collected, i.e., the lake consists of a finite number of water columns each of constant 1 cm^2 cross section. Volume changes may then be considered as consisting entirely of changes in length, and each component specific volume of

TABLE 1. *Compressibility coefficients and compression in unit volume* (C_t) *at temperatures between 0 and 30 degrees Centigrade, based on Amagat (1893)*

°C	Compressibility coefficient* ($cm^3/cm^3/atm$)	Compression in 1 cm^3 (C_t)* (cm^3/atm)
	$\times 10^{-6}$	$\times 10^{-6}$
0	52.50	52.50
1	51.95	51.95
2	51.60	51.60
3	51.30	51.30
4	51.05	51.05
5	50.80	50.80
6	50.60	50.60
7	50.43	50.43
8	50.27	50.27
9	50.13	50.13
10	50.00	50.00
11	49.85	49.85
12	49.75	49.75
13	49.64	49.64
14	49.53	49.53
15	49.44	49.44
16	49.35	49.35
17	49.30	49.30
18	49.22	49.22
19	49.15	49.15
20	49.10	49.10
21	49.05	49.05
22	49.02	49.02
23	48.98	48.98
24	48.93	48.93
25	48.90	48.90
26	48.88	48.88
27	48.85	48.85
28	48.82	48.82
29	48.81	48.81
30	48.80	48.80

* Second decimal places only approximate.

[2] The author is aware of Beyer's (1954) conclusion that Amagat's coefficients are slightly too large. The use of Amagat's coefficients may introduce a small systematic error.

TABLE 2. *Specific volume anomaly* ($10^5\delta_{t,p}$)*
(Specific volume length anomaly when applied to columns of 1 cm² cross section)

Depth		Pressure,	Temperature, °C							
feet	meters	atmospheres	0	1	2	3	4	5	6	7
0	0	0	13.0	7.0	3.0	1.0	0	1.0	3.0	7.0
	5	0.5	10.4	4.4	0.4	−1.6	−2.5	−1.5	0.5	4.5
	10	1.0	7.8	1.8	−2.2	−4.1	−5.1	−4.1	−2.1	2.0
	15	1.5	5.1	−0.8	−4.7	−6.7	−7.7	−6.6	−4.6	−0.6
50	15.2	1.52	5.0	−0.9	−4.8	−6.8	−7.8	−6.7	−4.7	−0.7
	25	2.5	−0.1	−6.0	−9.9	−11.8	−12.8	−11.7	−9.7	−5.6
100	30.5	3.05	−3.0	−8.8	−12.7	−14.6	−15.6	−14.5	−12.4	−8.4
	35	3.5	−5.4	−11.2	−15.1	−17.0	−17.9	−16.8	−14.7	−10.7
150	45.7	4.57	−11.0	−16.7	−20.6	−22.4	−23.3	−22.2	−20.1	−16.1
	50	5.0	−13.3	−19.0	−22.8	−24.7	−25.5	−24.4	−22.3	−18.2
	100	10.	−39.5	−45.0	−48.6	−50.3	−51.1	−49.8	−47.6	−43.4
	150	15.	−65.8	−70.9	−74.4	−76.0	−76.6	−75.2	−72.9	−68.7
	200	20.	−92.0	−96.9	−100.2	−101.6	−102.1	−100.6	−98.2	−93.9
	250	25.	−118.3	−122.9	−126.0	−127.3	−127.6	−126.0	−123.5	−119.1

Depth		Pressure,	Temperature, °C							
feet	meters	atmospheres	7	8	9	10	11	12	13	14
0	0	0	7.0	12.0	19.0	27.0	37.0	48.0	60.0	73.0
	5	0.5	4.5	9.5	16.5	24.5	34.5	45.5	57.5	70.5
	10	1.0	2.0	7.0	14.0	22.0	32.0	43.0	55.0	68.0
	15	1.5	−0.6	4.5	11.5	19.5	29.5	40.5	52.6	65.6
50	15.2	1.52	−0.7	4.4	11.4	19.4	29.4	40.4	52.5	65.5
	25	2.5	−5.6	−0.6	6.5	14.5	24.5	35.6	47.6	60.6
100	30.5	3.05	−8.4	−3.3	3.7	11.8	21.8	32.8	44.9	57.9
	35	3.5	−10.7	−5.6	1.5	9.5	19.6	30.6	42.6	55.7
150	45.7	4.57	−16.1	−11.0	−3.9	4.2	14.2	25.3	37.3	50.4
	50	5.0	−18.2	−13.1	−6.1	2.0	12.1	23.1	35.2	48.2
	100	10.	−43.4	−38.3	−31.1	−23.0	−12.9	−1.8	10.4	23.5
	150	15.	−68.7	−63.4	−56.2	−48.0	−37.8	−26.6	−14.5	−1.3
	200	20.	−93.9	−88.5	−81.3	−73.0	−62.7	−51.5	−39.3	−26.1
	250	25.	−119.1	−113.7	−106.3	−98.0	−87.6	−76.4	−64.1	−50.8

Depth		Pressure,	Temperature, °C							
feet	meters	atmospheres	14	15	16	17	18	19	20	21
0	0	0	73.0	87.0	103.0	120.0	138.0	157.0	177.0	198.0
	5	0.5	70.5	84.5	100.5	117.5	135.5	154.5	174.5	195.6
	10	1.0	68.0	82.1	98.1	115.1	133.1	152.1	172.1	193.1
	15	1.5	65.6	79.6	95.6	112.6	130.6	149.6	169.6	190.6
50	15.2	1.52	65.5	79.5	95.5	112.5	130.5	149.5	169.5	190.5
	25	2.5	60.6	74.6	90.7	107.7	125.7	144.7	164.7	185.7
100	30.5	3.05	57.9	71.9	88.0	105.0	123.0	142.0	162.0	183.0
	35	3.5	55.7	69.7	85.7	102.7	120.8	139.8	159.8	180.8
150	45.7	4.57	50.4	64.4	80.5	97.5	115.5	134.5	154.6	175.6
	50	5.0	48.2	62.3	78.3	95.4	113.4	132.4	152.5	173.5
	100	10.	23.5	37.6	53.7	70.7	88.8	107.9	127.9	149.0
	150	15.	−1.3	12.8	29.0	46.1	64.2	83.3	103.4	124.4
	200	20.	−26.1	−11.9	4.3	21.4	39.6	58.7	78.8	99.9
	250	25.	−50.8	−36.6	−20.4	−3.3	15.0	34.1	54.3	75.4

Depth		Pressure,	Temperature, °C							
feet	meters	atmospheres	21	22	23	24	25	26	27	28
0	0	0	198.0	221.0	244.0	268.0	294.0	320.0	347.0	375.0
	5	0.5	195.6	218.6	241.6	265.6	291.6	317.6	344.6	372.6
	10	1.0	193.1	216.1	239.1	263.1	289.1	315.1	342.1	370.1
	15	1.5	190.6	213.7	236.7	260.7	286.7	312.7	339.7	367.7
50	15.2	1.52	190.5	213.6	236.6	260.6	286.6	312.6	339.6	367.6
	25	2.5	185.7	208.7	231.8	255.8	281.8	307.8	334.8	362.8
100	30.5	3.05	183.0	206.1	229.1	253.1	279.1	305.1	332.1	360.1
	35	3.5	180.8	203.8	226.9	250.9	276.9	302.9	329.9	357.9
150	45.7	4.57	175.6	198.6	221.6	245.6	271.7	297.7	324.7	352.7
	50	5.0	173.5	196.5	219.5	243.5	269.6	295.6	322.6	350.6
	100	10.	149.0	172.0	195.0	219.1	245.1	271.1	298.2	326.2
	150	15.	124.4	147.5	170.5	194.6	220.7	246.7	273.7	301.8
	200	20.	99.9	123.0	146.0	170.1	196.2	222.2	249.3	277.4
	250	25.	75.4	98.5	121.6	145.7	171.8	197.8	224.9	253.0

* Decimals are only approximate.

each column may be considered to contain unit mass in a 'cube' of 1 cm^2 cross section and variable length. Thus compression effects may be subtracted from the specific volume at temperature to obtain the resultant length of the specific volume 'cube' at *in situ* temperature and pressure

$$a_{t,o} - \Delta a_{t,p} = \text{specific volume length } \textit{in situ} = a_{t,p}. \quad (4)$$

To reduce the physical size of the numbers it is convenient to work with the specific volume length anomaly which, further, is multiplied temporarily by 10^5.

$$a_{t,p} - 1.000000 = \text{specific volume length anomaly} = \delta_{t,p} \quad (5)$$

The computations leading to the tabulated (Table 2) specific volume length anomaly of water at 15° C and 25 meters depth will serve as an example of the way the table was constructed.

a at 15°, 0 hydrostatic pressure $= a_{t,o} = 1.00087$ cm³/gm (Eq. 1)

$p = 25$ meters ÷ 10 meters/atm $= 2.5$ atm (Eq. 2)

$\Delta a_{15,2.5} = pC_t = 2.5$ atm $\times$ 49.44 $\times 10^{-6}$cm³/gm/atm $= 123.6 \times 10^{-6}$cm³/gm (Eq. 3)

$a_{15,2.5} = (1.00087$ cm³/gm ÷ 1 cm²/gm) $- (123.6 \times 10^{-6}$cm³/gm ÷ 1 cm²/gm) $= 1.00087$ cm $- 123.6 \times 10^{-6}$ cm $= 1.000746$ cm (Eq. 4)

$\delta_{15,2.5} = 1.000746$ cm $- 1$ cm $= 0.000746$ cm (Eq. 5)

$10^5\delta_{15,2.5} = 74.6$ cm (see $t = 15°$, p = 2.5 atm in Table 2)

The specific volume length anomalies ($10^5\delta_{t,p}$) for each degree between 0 and 28° C and at several pressure levels are given in Table 2. This table is of minimal size so far as numbers of pressure levels are concerned. The user is advised to expand it by adding other pressure levels in the depth (pressure) range which pertains to his lake.

Computation begins with a fairly detailed reading of the temperature profile, in which the profile is broken down into its essentially linear portions and the temperature and depth (pressure) of each inflection point recorded. Enough inflection points should be read to reproduce the profile well when these points on a graph are connected by straight lines.

The required specific volume length anomaly for the surface temperature is found by interpolation between the proper values of Table 2. Similarly the anomaly for each inflection point is found, by single interpolation when the depth (pressure) falls on a tabulated pressure level, or by double interpolation when observed temperature and pressure both fall between tabulated values.

The anomaly is determined for the surface, for each inflection point, and for the reference level. The anomalies are averaged by successive pairs and each average is multiplied by the depth interval (in centimeters) covered by that pair to give the calculated length anomaly, ΔD, of that segment of the water column. Each ΔD is divided by 10^5 to return it to actual value; the ΔD's are summed cumulatively from zero at the surface down to the reference level; and the cumulated sum at the reference level is converted to meters (see Table 3). The cumulated length anomaly added to the reference level's depth under standard conditions gives the calculated length of the existing unit-cross-section water column. The final calculated length of the water column is its dynamic height or geopotential height. In Table 3 the reference level was the 60-decibar surface whose depth under standard conditions would be 60 meters.

At stations where the depth is less than that of the chosen reference level it is permissible to substitute the lower parts of a near-by station of adequate depth, as in Figure 4. When this is done the isobaric surfaces become horizontal (slopeless and currentless) between the identical parts of the two stations. This device was suggested by Nansen and introduced by Helland-Hansen (1934). It is apparently satisfactory in places where bottom currents are virtually absent, but may be seriously in error in places where currents

TABLE 3. *Dynamic height computation, Station 40, survey* Synoptic II, *27 July 1954*

Depth cm	Temperature °C	$10^5\ \delta_{t,p}$ at temp. & depth	Average	Depth interval	Product	ΔD, cm	Cumulative ΔD, cm	60-decibar ΔD	
								cm	meters
0	18.6	149.4					0		
			141.5	520	73580	0.74			
520	17.9	133.6					0.74		
			99.4	520	51688	0.52			
1040	13.8	65.2					1.26		
			49.0	480	23520	0.24			
1520	11.3	32.7					1.50		
			9.2	1530	14076	0.14			
3050	5.1	−14.3					1.64		
			−16.7	760	−12692	−0.13			
3810	4.4	−19.0					1.51		
			−21.0	760	−15960	−0.16			
4570	4.3	−23.0					1.35		
			−26.7	1430	−38181	−0.38			
6000	4.3	−30.3					0.97	0.97	0.010
			add reference level depth at standard conditions						60.000 meters
			Dynamic height in dynamic meters						60.010

along the bottom are significant. This device should be used only with great caution at stations so shallow that major parts of the water column require substitution of values.

Current directions are obtained by plotting the dynamic height for each station and drawing height contours of the surface topography at regular intervals. Current-direction arrowheads may be drawn on the contour lines by application of the geostrophic principle: the currents are situated on the slopes of the topography, flow parallel to the contours, and flow in such direction that the topographic 'high' is on the right (in the Northern Hemisphere) when the observer looks in the direction of flow.

Current velocity between each pair of stations can be obtained from: $v = 10\ i_d/0.000145 \sin \phi$ (Sverdrup *et al.* 1942: 392) where i_d is the slope of the surface between the stations and sin ϕ is the natural trigonometric function of the latitude of the mid-point between the station pair. If the slope is expressed in meters of height difference per meter of horizontal distance between the stations, the velocity will be in meters per second; if the slope is in cm/m, velocity will be in centimeters per second. LaFond (1951: 98) gives a similar method of calculating current velocity from the same parameters.

Since the distance between contours is inversely proportional to the velocity, it is convenient to determine the velocities of the fastest current, the slowest current, and of a few intermediate ones, then to construct a trumpet-shaped graph (see Figs. 1, 2, and 3) from which velocity may be read by transferring the intercontour distance with dividers.

APPLICATIONS OF THE METHOD

The dynamic height method has been used to determine the surface current patterns and velocities in Lake Huron at three different times in the summer of 1954. At the end of June the major part of the lake was still in essentially its spring condition —with no thermocline yet formed. At this time the current pattern (Fig. 1) was almost identical to that deduced by Harrington (1895) from drift bottles released by lake steamers throughout the entire shipping season, approximately late March to early December. It was also in agreement with the results of Millar (1952) who confirmed Harrington's current pattern by studies of intake-water temperatures on lake steamers throughout the shipping season. For these reasons it is believed that the pattern observed in June approximates the "fundamental" winter-to-winter circulation pattern of the lake.

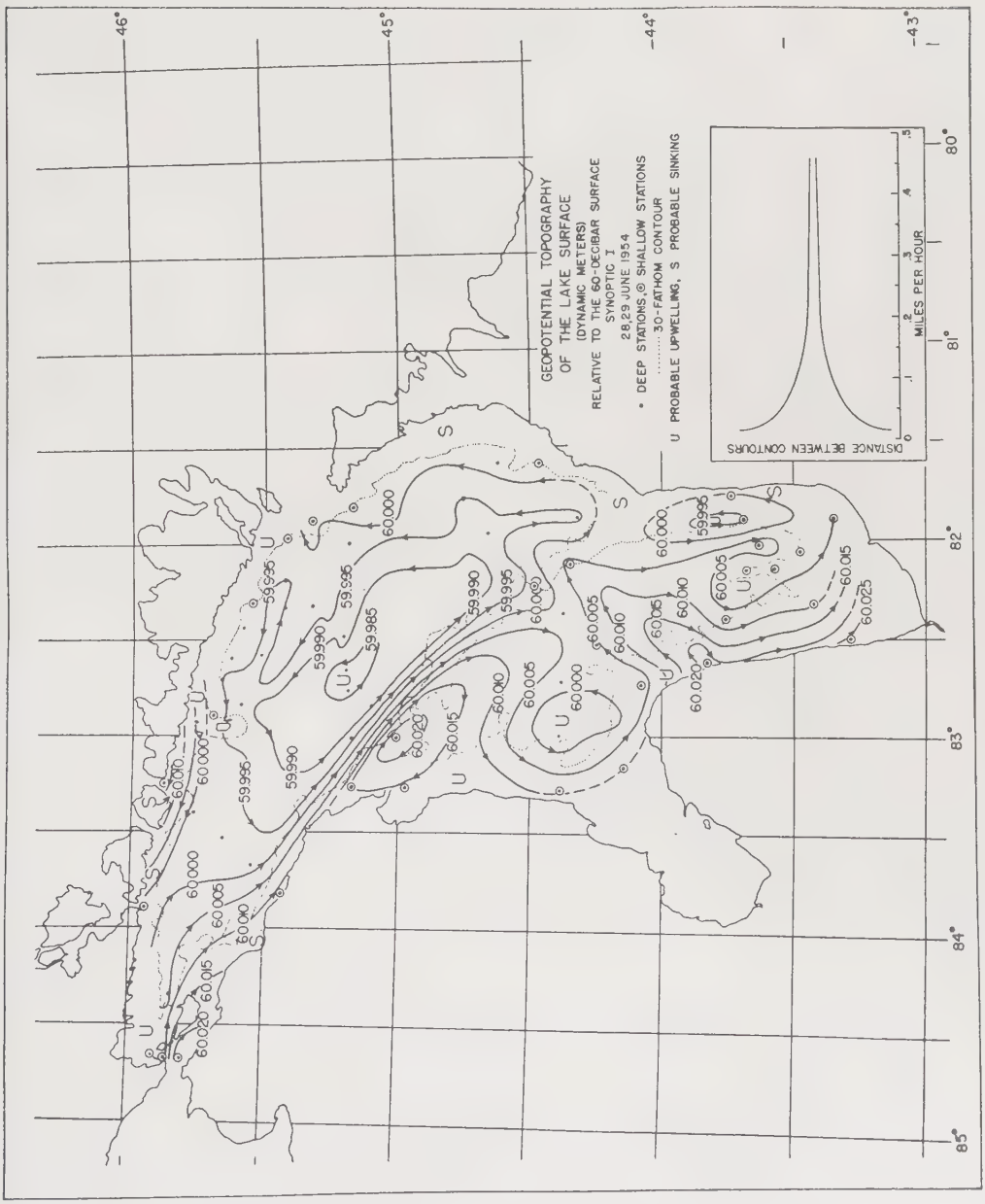

FIG. 1. The currents of Lake Huron on 28–29 June 1954, in relation to the 60-decibar surface.

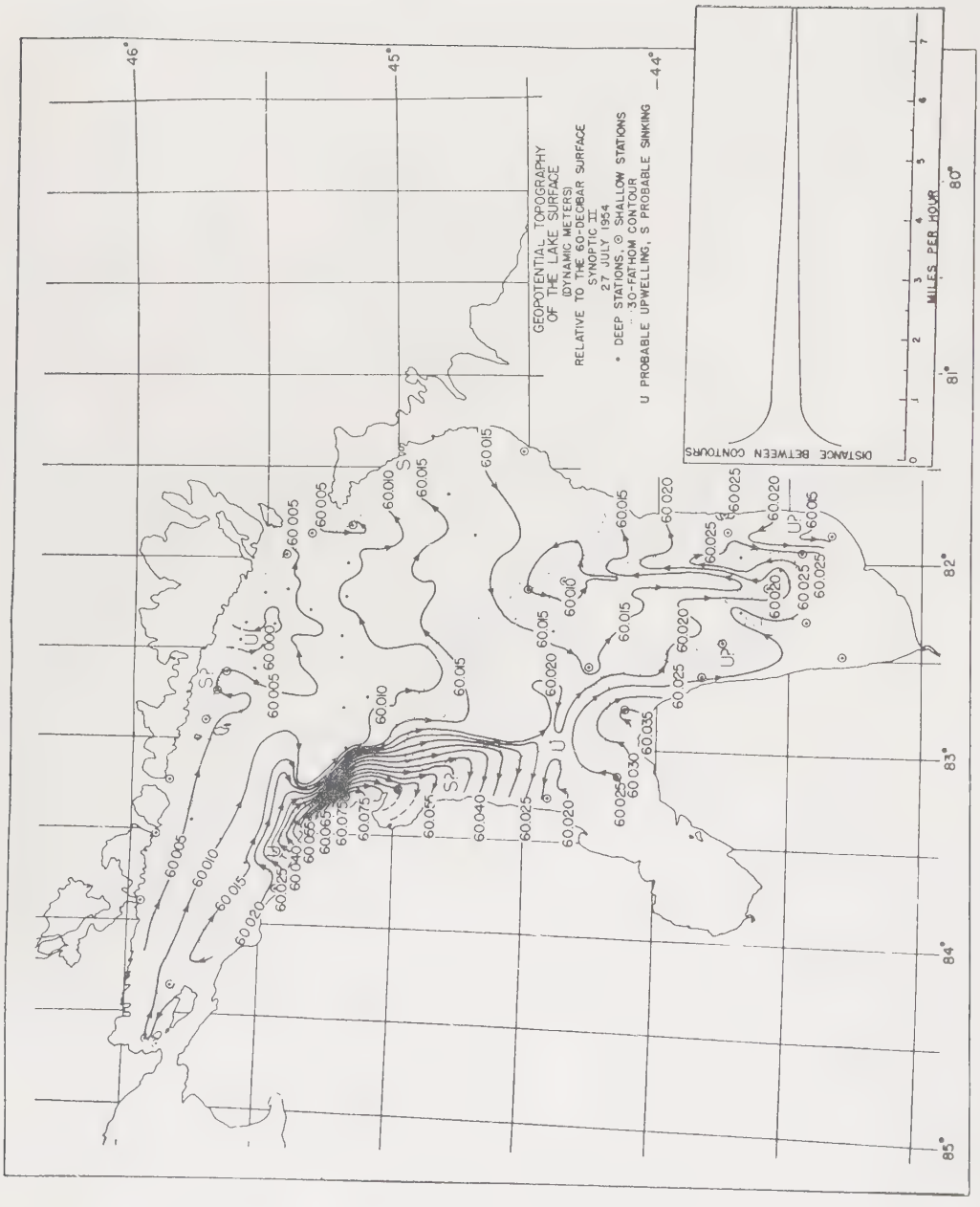

FIG. 2. The currents of Lake Huron on 27 July 1954, in relation to the 60-decibar surface.

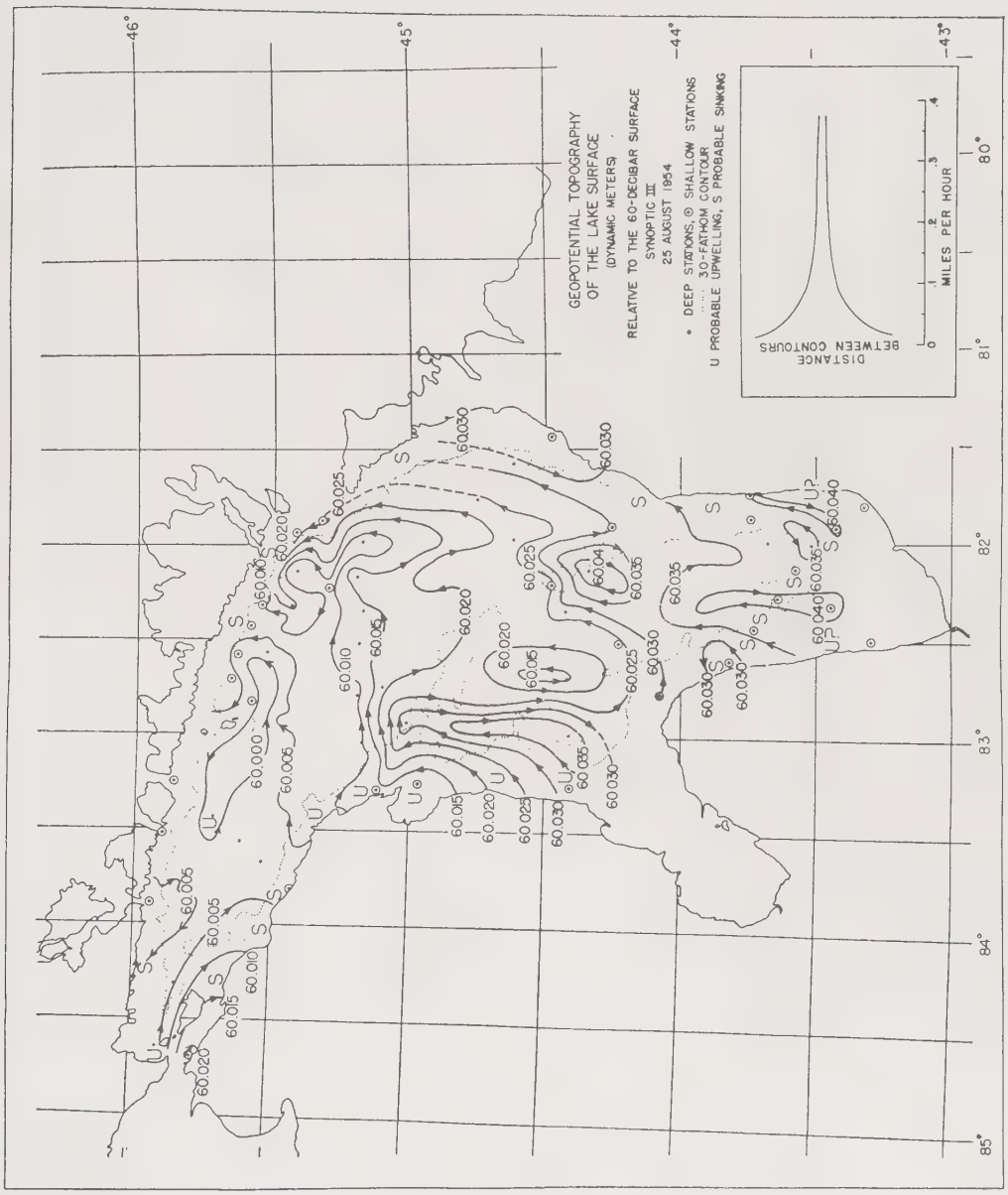

FIG. 3. The currents of Lake Huron on 25 August 1954, in relation to the 60-decibar surface. This is apparently a non-equilibrium condition.

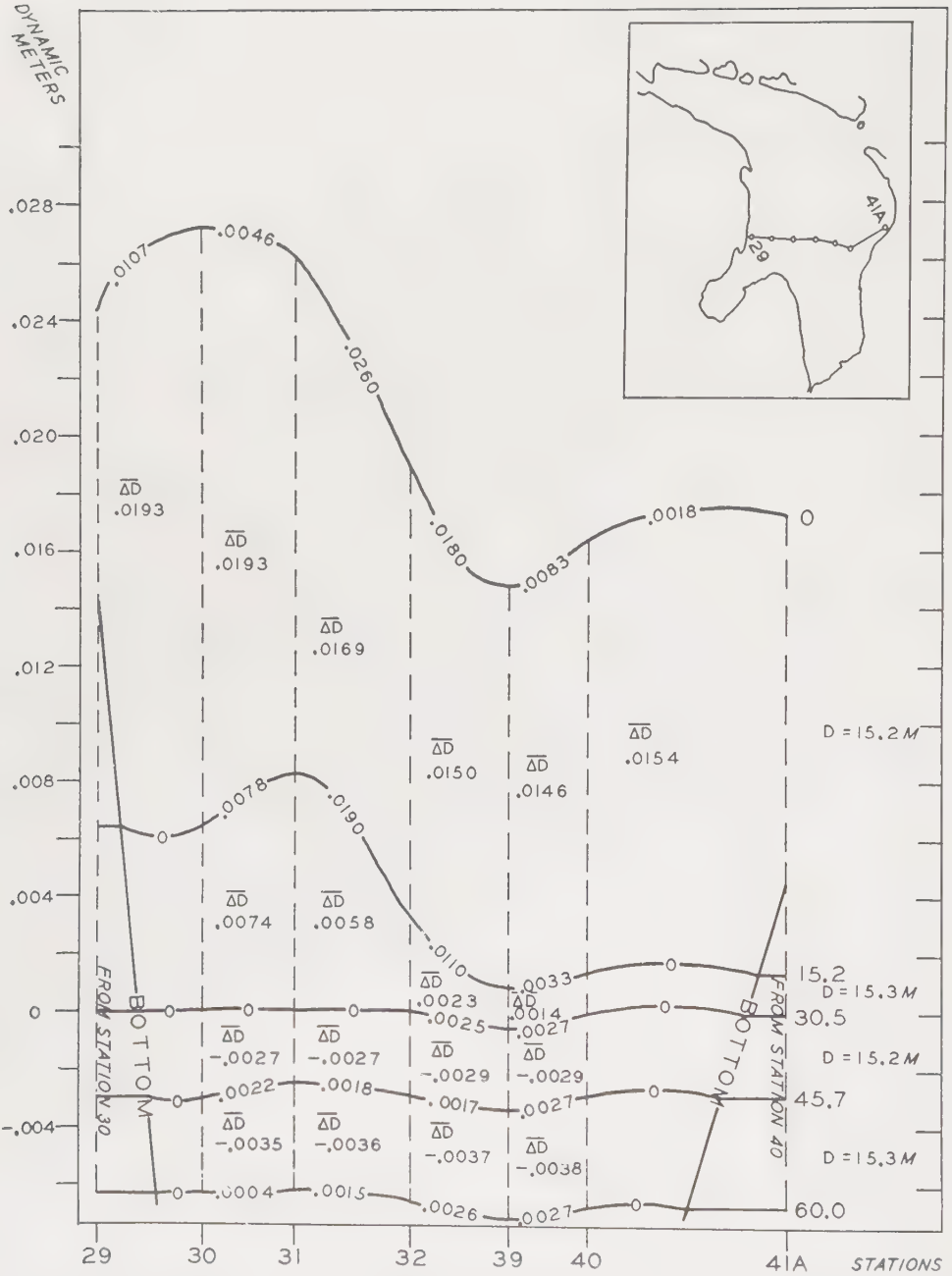

FIG. 4. The distribution of dynamic heights and current velocities in the Oscoda, Michigan-Southampton, Ontario section on 27 July 1954. Current velocities in meters/second are shown on the decibar surfaces. The ΔD values, in dynamic meters, in the between-station intercontour blocks are averages applying to those blocks. Interception of the isobaric surfaces by the bottom is indicated at each end. D values on the right are the intercontour intervals, in meters, under standard conditions. The insert shows the location of the section.

In the interval from late June to late July a strong thermocline developed over the whole lake. The survey of 27 July took place after winds from quarters more northerly than usual, and the current pattern (Fig. 2) appeared to be a wind-induced distortion of the fundamental pattern; the warm light surface water apparently responded rather readily to the wind shift.

Prior to the survey of 25 August 1954 (Fig. 3) the winds were from more nearly normal westerly quarters, and the current pattern appeared to indicate a partial return toward the June condition. The fact that the outflows from Lakes Michigan

TABLE 4. *Computation of water transport through the Oscoda-Southampton section, 27 July 1954*
Data for second and fourth columns are from Figure 4.

Isobaric surface pair, decibars	Intersurface depth $(D + \Delta\bar{D})$, dynamic m*	Intersurface area m²	Average velocity m/sec*	Transport m³/sec**	Transport sum m³/sec**
		Transport between stations 29 and 30, 23979 meters apart			
0–15.2	15.2193	364943	0.0054	1970 north	
15.2–30.5	—	—	0	0	
30.5–45.7	—	—	0	0	
45.7–60.0	—	—	0	0	
					1970 north
		Transport between stations 30 and 31, 21243 meters apart			
0–15.2	15.2193	323304	0.0016	517 north	
15.2–30.5	15.3074	325175	0.0039	1268 north	
30.5–45.7	15.1973	322836	0.0011	355 north	
45.7–60.0	15.2965	324944	0.0013	422 north	
					2562 north
		Transport between stations 31 and 32, 26393 meters apart			
0–15.2	15.2169	401620	0.0225	9036 south	
15.2–30.5	15.3058	403966	0.0095	3838 south	
30.5–45.7	15.1973	401102	0.0009	361 south	
45.7–60.0	15.2964	403718	0.0017	686 south	
					13921 south
		Transport between stations 32 and 39, 22048 meters apart			
0–15.2	15.2150	335460	0.0145	4864 south	
15.2–30.5	15.3023	337385	0.0068	2294 south	
30.5–45.7	15.1971	335066	0.0021	704 south	
45.7–60.0	15.2963	337253	0.0022	742 south	
					8604 south
		Transport between stations 39 and 40, 17703 meters apart			
0–15.2	15.2146	269344	0.0058	1562 north	
15.2–30.5	15.3014	270881	0.0030	813 north	
30.5–45.7	15.1971	269034	0.0027	726 north	
45.7–60.0	15.2962	270789	0.0027	731 north	
					3832 north
		Transport between stations 40 and 41A, 44096 meters apart			
0–15.2	15.2154	670938	0.0009	604 north	
15.2–30.5	—	—	0	0	
30.5–45.7	—		0	0	
45.7–60.0	—	—	0	0	
					604 north
				Net transport, m³/sec	13557 south

* Last decimal place only approximate.
** Last two places only approximate.

and Superior, in flowing through Lake Huron, would have to cross dynamic height contours in both the upper and lower ends of the lake indicates that this survey covered a transient non-equilibrium condition in the lake.

The surface current directions of all three surveys were in excellent agreement with the movements of drift bottles released on the days of the surveys. Average current velocities obtained by the dynamic height method in June and July were not significantly different, statistically, from those of drift bottles released on those surveys. From the August survey, drift bottle returns were too few to permit velocity comparison.

As a further check on the method, a water transport estimate has been made for the 27 July section from Oscoda, Michigan, to Southampton, Ontario (Fig. 4). If the method is correct, summation of the products of average velocity and area from the component parts of the section should give a rough measure of the volume of water passing through the section. This volume was compared with the outflow of Lake Huron via the St. Clair River. The distribution of dynamic heights across the section, average dynamic height increments in between-station blocks, and velocities between station pairs are shown in Figure 4; the computations are summarized in Table 4.

Current velocity was calculated at each of the 0, 15.2, 30.5, 45.7, and 60.0 decibar surfaces between each pair of stations in the section. An average velocity was obtained for each intercontour area between each pair of stations; each intercontour average dynamic height increment, $\overline{\Delta D}$, between each pair of stations was added to the corresponding standard-condition depth interval, D, and multiplied by the distance between stations to give the area of each intercontour between-station block; the average velocity in each block was multiplied by the block area; and the resulting volume transports were summed algebraically. The resulting estimate of transport through the section was about 13,500 m^3/second or about 473,000 ft^3/second. In the last week of July 1954 the outflow of the St. Clair River was 216,000 ft^3/second (U. S. Lake Survey, Detroit, personal communication). The order-of-magnitude agreement between these figures is probably all that could be expected, for there are areas between the section ends and the shores, and below the reference level, where no transport figures could be obtained; in addition, the Helland-Hansen substitutions in the bottoms of the end stations force the supposition of no currents or transports there.

POTENTIAL ERRORS OF THE METHOD

Sverdrup *et al.* (*op. cit.*, pp. 393–4) review the sources of potential error in the dynamic height method, and every user of the method should be familiar with them. They include errors stemming from the neglect of frictional effects and errors due to the slope of the reference surface. Currents obtained from dynamic computations are relative to any currents at the reference level. In considering these relative currents as *absolute* currents an error is introduced if the reference surface slopes (has currents). Errors from these sources appear to be small in the ocean, and (in the first approximation) may be considered small in lakes that are wide in comparison to the inertia circle, whose radius is: $r = v/2\omega \sin \phi$ (where v is maximum surface velocity and $2\omega \sin \phi$ is the double angular velocity of the earth in that latitude).

The presence of internal seiches or internal waves during the period of observation may be a source of potential error, but the works of Mortimer (1951, 1954, 1955) indicate that in large deep lakes the periods of such oscillations are long compared to the ordinary work-day. In the first approximation, internal seiches of large deep lakes may be considered to cause little error in one-day synoptic surveys such as were used on Lake Huron. Their effect on the accuracy of the method in smaller shallower lakes remains to be investigated.

The most probable source of significant error in applications of the dynamic height method to lakes appears to be the direct

effect of the wind. Pronounced changes in wind direction and/or velocity produce changes in the distribution of density, and significant accelerations (not taken into account by the method) may be present until equilibrium is regained. Prolonged relatively constant winds may remove surface water from the up-wind shore and pile it against the down-wind shore, imparting an 'artificial' slope to the surface. The lee-shore sinking and windward-shore upwelling produced by such winds may be expected to tilt subsurface isobaric surfaces in the opposite direction from the surface slope—further increasing the depth of warm surface water down-wind and decreasing it up-wind. Further studies on the effect of the wind, and upon the degree to which shallowness of lakes limits the use of the method, are needed.

CONCLUSIONS

Although many potential sources of error are to be considered in applications of the dynamic height method, most of them appear to lead to relatively small errors and nearly all may be minimized by careful planning and by choice of days for observation. Used with proper caution, the dynamic height method appears to be a promising technique for the investigation of certain circulation phenomena, in large lakes at least. The method appears to be more satisfactory for determinations of surface current patterns and velocities than for subsurface water transport computations. Application of the method in Lake Huron has produced logical and reasonable results which are both internally consistent and in good agreement with the behaviors of other parameters (Ayers *et al.* 1956).

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Benthic Productivity as Influenced by Fish Predation*

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ABSTRACT

Sampling of benthic organisms was carried out in two similar, one-acre ponds in southern Michigan throughout the open water period of 1951. The bottom fauna in each pond was sampled by means of 20 Ekman dredge collections each week. This sampling scheme was found capable of detecting a difference between two populations when the ratio of their magnitudes is 1.9.

Fish were present in one of the ponds in the first half of the summer. These were then transferred from this pond to the second pond in early July. Rates of growth of the fish and the bottom organisms were estimated and the production calculated at both trophic levels. The apparent rate of change of bottom fauna biomass was assumed to reflect a basic rate of increase varying inversely with the biomass level, minus the rate of fish predation.

Calculated production of 811 pounds of fish-food and 181 pounds of fish are shown to be of reasonable order as compared with other studies, with the fish-food probably underestimated. A factor not included in the calculations was the effect of emergence of aquatic insects.

The average production of bottom fauna fish-food during a growing season amounted to about 17 times the standing crop, when fish were present. In the absence of fish, the apparent production rate of fish food decreased and finally stopped at a higher level of standing crop. In the presence of fish, the standing crop of fish food was depressed and the rate of production increased.

INTRODUCTION

Aquatic food-cycle relationships between populations of benthic organisms and the fish populations preying upon them have been considered by several workers. Lindeman (1942) in his trophic-level concept discussed the energy flow from one level to another. Clarke (1946) recognized the importance of benthos in the food cycle of Georges Bank and pointed out the need for quantitatively reliable information on the size of the standing crop and the rates of production of the various components of the bottom fauna.

Knowledge of the growth of populations of aquatic organisms and understanding of the predator-prey relationships are of basic importance in aquatic biology. It has been pointed out repeatedly that the most important aspect of this link in the aquatic trophic system is the true productivity of the biomass of food organisms, not simply size of the standing crop. Most investigators, lacking a measure for productivity, have been forced to conclude with Ricker (1946), concerning standing crop, that "such a measure is certainly more useful than none at all".

Attempts to study the dynamics of production in invertebrate fish-food populations seem to fall under three principal categories, as follows:

1. Direct study of the dynamics of the bottom fauna itself. Only Borutsky (1939), Lundbeck (1926) and Miller (1941) were credited by Ricker (1946) with factual studies of production rather than measurements of the standing crop of bottom organisms.

2. Study of the growth of fish, and of the metabolic requirements of the fish for growth and maintenance, reasoning thence to the amount of food required to satisfy these requirements. Allen (1951) and Gerking (1954) have reported such studies.

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3. Estimation of the total amount of food passing through the fish population by studying the food habits of fish and the rate of clearance of the stomach contents, and a comparison of this quantity with the prey population producing it. Ricker (1937, 1946) has pointed out the possibilities of this method.

An experimental attack on the problem is reported here. Briefly, the bottom fauna was appraised at intervals over a growing season in two similar, one-acre ponds, one of which contained a population of fish at the beginning of the experiment, while the other pond was started without fish. Halfway through the season the fish were removed from the one pond and placed in the other, and the effects of this change were observed. The present study comes most nearly under the first heading above, since we have followed the bottom fauna population, and have observed how it changed with variation in the predation pressure exerted by the fish. Our information on productivity is thus inferred rather than direct. We have also been able to compare the computed production of fish food with the growth achieved by the fish.

MATERIALS AND METHODS

The ponds

Ponds 4 and 5 at the Wolf Lake State Fish Hatchery, ten miles west of Kalamazoo, Michigan, were selected because they were similar in size, depth, basin conformation, bottom type, and common water supply. The ponds each had a surface area of approximately one acre, a maximum depth of 6.5 feet, and an average depth of 3.0 feet. The water supply was high in carbonate hardness (160 ppm) and came directly from a large spring. A nearly uniform water level was maintained with a minimum of overflow. The temperature remained relatively constant at about 70°F during the experiment. Black organic muck covered the bottoms of both ponds except for the narrow sandy shore line. Most of the bottom of each pond became covered with *Chara*, the only other rooted vegetation being a bed of *Potamogeton pectinatus* near the outlet of Pond 4. A Secchi disk was visible at the bottom of each pond throughout the experiment except for one ten-day period when a plankton bloom developed in Pond 4. Both ponds had been empty for a time prior to the beginning of the experiment.

The fish

The fish population was made up of three species of sunfish: bluegills (*Lepomis macrochirus*), pumpkinseeds (*Lepomis gibbosus*), and redear sunfish (*Lepomis microlophus*), all from the Wolf Lake Hatchery pond stock. These species were selected because of their known dependence upon the invertebrate benthic fauna for food. Most of the fish were young of the previous year, with some larger fish, and ten very large bluegills. It was necessary to hold the fish without food for 18 days before beginning the experiment. The fish were in Pond 4 from April 21 to July 3, then in Pond 5 from July 9 to September 9, 1951. With between 2900 and 2100 fish present, the total weight varied between 134 and 194 pounds (see Table 4 for details). Some (uncounted)

TABLE 1. *Numbers and weights of fish in the ponds at the beginning and at the end of the two phases of the experiment*

Species and time in pond	Number and total weight of fish in ponds					
	At planting		At removal		Removed for food studies	
	Number	Weight (lbs)	Number	Weight (lbs)	Number	Weight (lbs)
Pond 4 (73 days)						
April 21–July 3						
Bluegills	1935	84.0	1535	133.7	68	5.5
Large bluegills	10	8.4	10	8.0	—	—
Pumpkinseeds	933	40.0	588	49.4	43	4.0
Redears*	60	1.8	52	3.5	3	0.2
Total, Pond 4	2938	134.2	2185	194.6	114	9.7
Pond 5 (62 days)						
July 9–Sept. 9						
Bluegills	920	88.5	591	94.5	53	8.8
Large bluegills	10	7.6	10	7.5	—	—
Pumpkinseeds	617	41.9	515	58.5	30	3.7
Redears	52	3.5	44	5.8	3	0.4
Total, Pond 5	1599	144.5	1160	166.3	86	12.9

* Redears in Pond 4 for 50 days, planted May 14.

thousands of fry were removed from Pond 4 at draining. Pond 5 received no fry and relatively few were produced there. These small fry were considered to have had a negligible effect upon the bottom fauna of the ponds. Those fish that died on the day of release and on the day immediately following were recovered and weighed, and replaced by an exactly equal weight of fish of approximately the same size. As a result, the information given in Table 1 concerning numbers of fish planted is not precise, but is approximately correct. By use of hook-and-line fishing and by seining, a number of fish were removed for study of food habits at various times throughout the experiment (Table 1).

Computation of growth rates

The rates of growth and of mortality are here compared as instantaneous rates. This method of dealing with problems of relative change and its advantages have been discussed in relation to aquatic populations by Ricker (1946, 1948), in terms of growth by Brody (1945), and in a more general way by a number of authors, including Neyman (1950). In the present study the principal advantage is that instantaneous rates allow the arithmetic addition of the effect of the various factors, such as growth and mortality, both of which are logically proportional in action. From the point of view of computation, an instantaneous rate is the natural logarithm of the surviving fraction, with the understanding that in the event of growth the "surviving fraction" exceeds unity and the natural logarithm is, therefore, positive, while in the event of mortality the fraction is less than unity and the logarithm, therefore, negative. In the present study the negative sign is held in the event of mortality or of loss of weight, rather than changed to a positive sign as is perhaps the more usual practice. This minor change in convention has been found useful in relating an instantaneous rate to its biological meaning.

GROWTH OF FISH

The growth achieved by these fish is an important aspect of this study. Two aspects of growth of the different species are shown in Table 2 as instantaneous rates (1) of growth of species biomass, and (2) of growth of individual fish. The "biomass growth rate" of Ivlev (1945) is the "net rate of increase or decrease of population" of Ricker (1946), and was computed here from the weight of fish present at the beginning and at the end of each phase of the experiment. The estimation of the instantaneous rate of growth achieved by individual fish was computed from average weights at the beginning and the ending of the two phases of the experiment. These instantaneous rates of growth based upon average weights of fish are approximate not only because they are based upon the inexactly-known numbers of fish but also because the populations of fish were mixed in size and presumably in rates of growth. To counterbalance this possible objection, it may be stated that most of the bluegills and pumpkinseeds and all of the redear sunfish were of a single age class. Use of these instantaneous rates implies constancy of growth rate over these periods, an assumption made necessary by the nature of the data.

TABLE 2. *Instantaneous rates of growth for species biomass and for individuals, and production of fish, both net and gross*

Species	Instantaneous rates of growth, on daily basis		Production of fish, in pounds	
	Of biomass	Of individuals	Net	Gross
In Pond 4:				
Bluegills	.00637	.00954	49.7	74.4
Large bluegills	−.00067	−.00067	−0.4	−0.4
Pumpkinseeds	.00289	.00922	9.4	30.0
Redears	.01330	.01616	1.7	2.1
Total, Pond 4	.00509 (mean)	.00912 (mean)	60.4	106.1
In Pond 5:				
Bluegills	.00106	.00820	6.0	46.5
Large bluegills	−.00021	−.00021	−0.1	−0.1
Pumpkinseeds	.00538	.00830	16.6	25.6
Redears	.00815	.01084	2.3	3.1
Total, Pond 5	.00260 (mean)	.00778 (mean)	24.8	75.1

The production of fish flesh reflects these rates of growth. The net production shown in Table 2 is the observed increase in the weight of the species biomass. The gross production of fish, on the other hand, makes

allowance for the fact that mortality by removing a certain weight of fish conceals a part of the true elaboration of fish flesh that occurred. The gross production of fish has been calculated following Ricker (1946) and Allen (1950). The relationship of the two kinds of production reduces to the fact that when using instantaneous rates, the gross production equals the net production multiplied by the ratio of the individual growth rate to the biomass growth rate. These estimates of gross production suffer from the same uncertainties as affect the individual instantaneous rates of growth.

WEIGHT OF FISH PRESENT

The effect exerted upon the bottom fauna at any time by the fish presumably varied with the weight of fish present, and this weight varied throughout the experiment as fish grew. The weight present at the median date between successive sets of bottom samples has been estimated (assuming a uniform rate of growth), and these weights are shown in Table 5. Use of this information will be made below in studying the influence of fish upon the bottom fauna.

FOOD HABITS OF THE FISH

Fish for study of food habits were collected throughout the study (Table 1). After the captured fish were measured, the stomachs were removed immediately and placed in alcohol, to stop digestive action. An effort was made to capture fish of all sizes present for this study of food habits.

Of 200 stomachs examined, only 14 were empty. Plant materials, mostly *Chara*, were found in a quarter of those stomachs with food, the plants making up about ten per cent of the volume of all food. Food habits of the three species were generally similar except for greater use by pumpkinseeds of snails and beetle larvae, and greater use by redears of snails and fingernail clams (*Pisidum*).

Numerically, the most important food groups were midges, mayflies, small cladocera, the fingernail clam, and coleopterous larvae of the family Haliplidae. The midges were consistently present in greater numbers in the stomachs than might be expected from their relative occurrence in bottom samples.

THE BOTTOM FAUNA

Fluctuations in the invertebrate fauna of the pond bottoms were followed by means of samples taken with a six-inch-square Ekman dredge. In each pond, 20 samples were taken so as to sample the various depths of the pond at each time of sampling. Such series of samples were taken at intervals of approximately one week throughout the experiment for a total of 340 samples in Pond 4, and 320 in Pond 5. The mean dates of sampling may be judged approximately from Figures 1 and 2. The dates of sampling in the two ponds did not coincide exactly, due to the time required for the sampling. The contents of each dredge were washed over a 30-mesh to the inch screen and the organisms sorted alive. The preserved organisms were later sorted to convenient taxonomic groups, usually family, counted and the volume measured by liquid displacement.

The exact distribution of forms by taxonomic group is not given here but may be found in Wilkins (1952). The most important groups by volume were mayflies, snails, oligochaetes, midges, and caddisflies in both ponds, and especially in Pond 5 the fingernail clam (*Pisidium*).

In analysis of the effect of fish upon the bottom fauna, the invertebrates have been divided into two groups—the fish food, and the non-fish-food. The fish-food organisms include all organisms collected except the leeches, oligochaetes, *Hexagenia* sp., and snails larger than those found in the fish stomachs analyzed. This division of the fauna follows previous work (Ball 1948); the exact division here is governed by presence or absence in the stomachs collected during the experiment.

The standing crop of the bottom fauna of the two ponds during the experiment is shown graphically in Figures 1 and 2, showing separately the fish-food and the non-fish-food levels, respectively. These graphs have been drawn with a logarithmic ordinate scale so that the slope of the line connecting successive sampling determinations

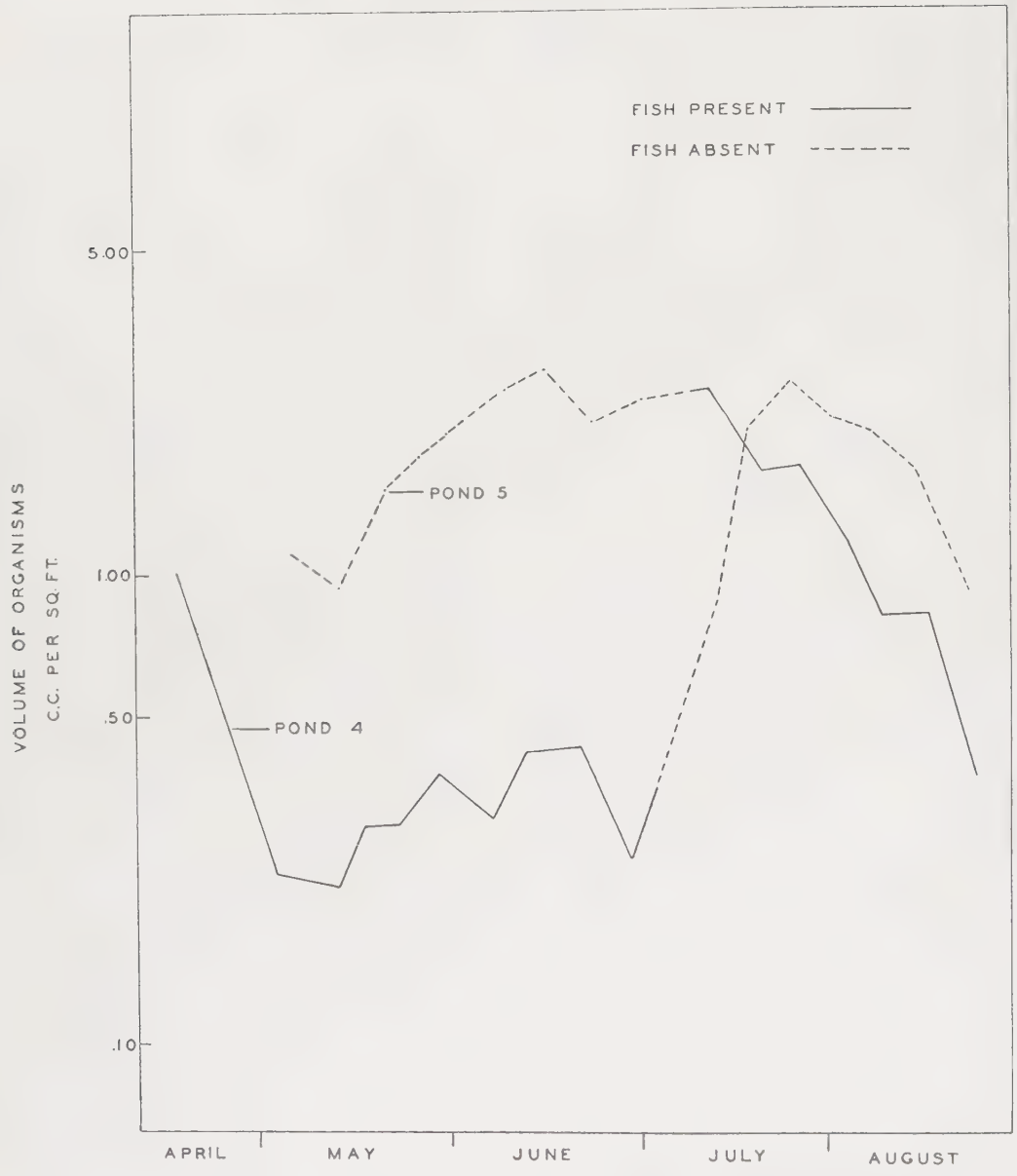

FIG. 1. Fluctuations in volume of standing crop of those bottom organisms *utilized* by the fish.

indicates the rate of change of the population in a relative sense, proportional to the instantaneous rates of change, which are shown for fish food in Table 3.

An analysis of variance of the fish-food data from bottom sampling is presented in Table 4. This table is included since so little has been offered as to size of adequate samples and the variability of bottom sampling. It supports the following discussion of sampling characteristics of these field methods. Further, from Table 4 it is clear that there were highly significant differences in fish-food volume among times of sampling. Data referred to here are shown in Figure 1.

A logarithmic transformation of the data was used for the same reasons as discussed

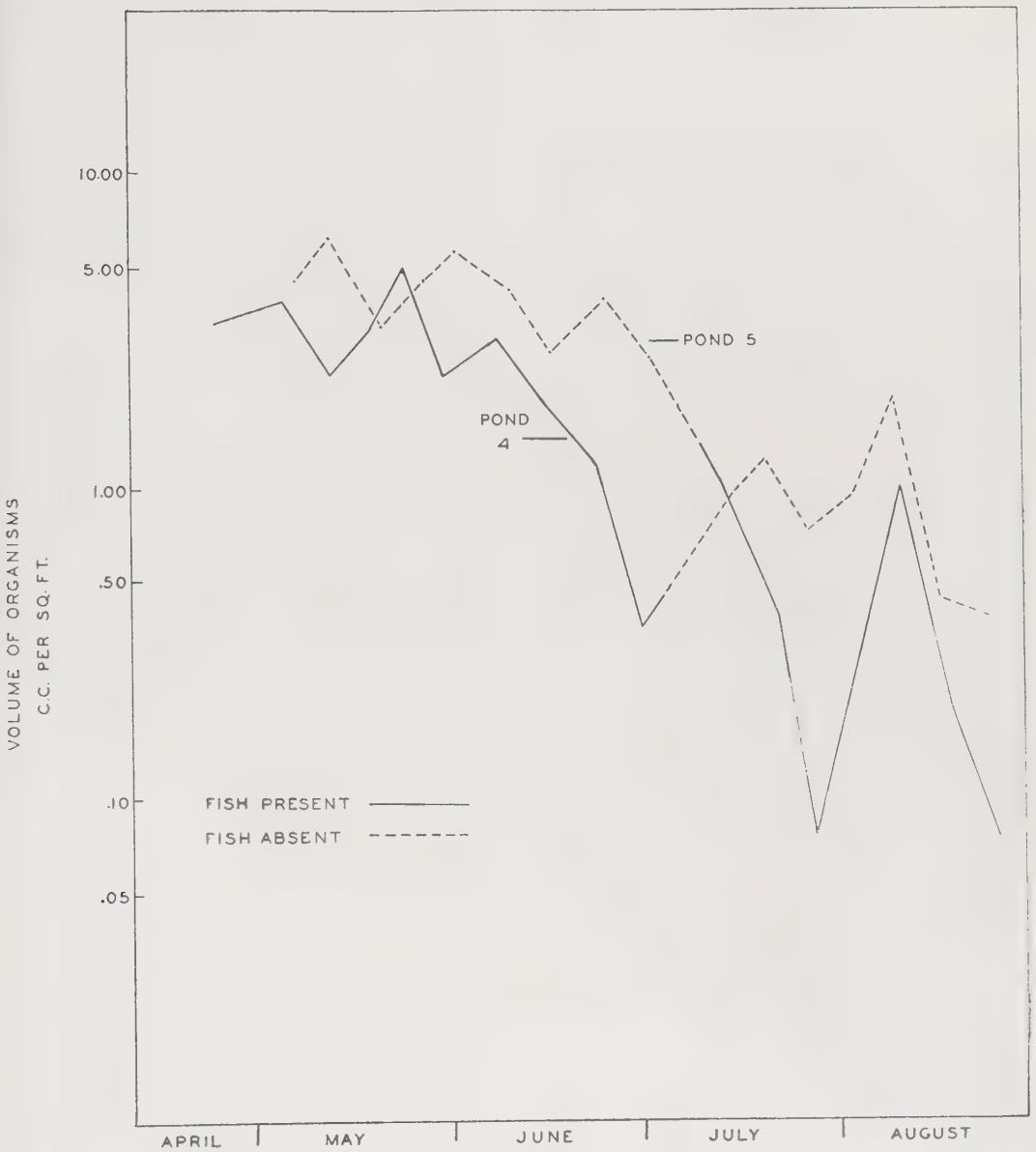

FIG. 2. Fluctuations in volume of standing crop of those bottom organisms *not utilized* by fish.

previously (Ball and Hayne 1952). One result of using this transformation is that if desired, confidence intervals could be plotted on Figure 1 as equal distances regardless of the magnitude of the mean value observed. Another consequence is that if natural logarithms are used in the analysis, then the difference between two means is the instantaneous rate of change stated in terms of the period concerned. The standard error of the difference between the two means becomes the standard error of the estimate of instantaneous rate of change, allowing some judgment concerning the characteristics of this sampling procedure for determining instantaneous rate of change. A further consequence of use of a logarithmic transformation is that

TABLE 3. *Observed and calculated instantaneous rates of change in fish-food biomass, and lengths of periods*

Period (month and week)	Pond 4			Pond 5		
	Length of period (days)	Instantaneous rate (on daily basis)		Length of period (days)	Instantaneous rate (on daily basis)	
		Observed	Calculated		Observed	Calculated
April 4	10	−.153	.023			
May 1	8	−.007	.040	6	−.030	.062
May 2*	5	.059	.029	7	.071	.056
May 3*	6	.004	.020	7	.020	.042
May 4*	7	.035	.011	6	.023	.033
June 1*	8	−.029	.003	9	.023	.022
June 2*	6	.058	−.006	6	.022	.008
June 3	8	.001	−.020	9	−.034	.015
June 4*	8	−.069	−.021	7	.017	.022
July 1*	14	.089	.136	11	.004	.000
July 2*	5	.176	.126	9	−.048	−.025
July 3*	7	.032	.055	6	.006	−.013
July 4	8	−.021	.049	8	−.045	−.007
August 1	5	−.014	.070	6	−.063	.007
August 2	8	−.029	.092	8	.001	.011
August 3	8	−.070	.135	7	−.111	.017

* Data from these periods used in multiple regression analysis.

TABLE 4. *Analysis of variance of natural logarithms of volumes of fish-food organisms, based on series of 20 samples taken from each pond at approximately weekly intervals*

Source of variability	Degrees of freedom	Mean square
Pond 4:		
Among 17 times of sampling	16	15.613
Within times of sampling	322	0.566
Pond 5:		
Among 16 times of sampling	15	5.094
Within times of sampling	304	0.482
Pooled error estimate from both ponds:		
Within times of sampling	626	0.525

Estimated standard deviation of a single determination = 0.724, equivalent to a coefficient of variation of 106 per cent.

Estimated standard error of a mean of 20 samples = 0.162, equivalent to a coefficient of variation of 18 per cent.

the standard error cannot be stated directly in the original units of measurement, but may be interpreted approximately in terms of coefficient of variation (Winsor and Clarke 1940).

In the present study, for example, using a combined estimate of variance from Table 4, the standard error of a series of 20 bottom samples may be estimated at 0.162, equivalent to a coefficient of variation of the mean of about 18 per cent. At the 95-per cent level a difference between (logarithmic) means of 0.458 (equivalent to a ratio of 1.58) may be judged larger than reasonably attributable to chance. Finally, we may state that with series of 20 bottom samples, with populations similar in variability to those observed here and working at the 95-per cent level, we may be reasonably sure (power of the test: 80 per cent, see Hald 1952) that if a difference of 0.642 logarithmic units is present between two populations, then this difference will be detected by our test. This characteristic, the ability to detect a true difference of stated magnitude, measures the reliability of the sampling methods used. The difference here, representing a ratio of the larger to the smaller population of 1.90, reflects the well known variability encountered in benthic sampling.

The biomass of fish food may be read from Figure 1 and that of non-fish-food organisms from Figure 2. The non-fish-food organisms made up a large part of the total bottom fauna sampled by the dredge, but they were either unavailable to the fish or rejected by them, for they were not found in the stomachs.

The fish-food organisms are here treated as one community biomass, even though made up of numerous species. Instantaneous rates of change have been computed for this fauna (Table 3), based upon the volume at the beginning and at end of each interval. The objective of this section is to relate these observed rates of change to such factors as were measured.

The general picture of changes in the biomass of fish food may be seen in Figure 1, where the semi-logarithmic scale allows visual comparison of rates of change. After the starved fish were introduced into Pond 4 in late April, the fish food decreased rapidly, reaching the lowest level of the experiment, and then increased gradually until the middle of June when two periods of pronounced decrease drove the population down almost to the low level reached in early May. At this time the fish were

removed according to prearranged plan. Pond 5, without fish during this first phase of the experiment, gained in fish-food biomass more rapidly during May than did Pond 4, to judge by the over-all trend, but later gained less rapidly. After the fish were placed in Pond 5 in early July, the fish-food biomass decreased continuously until the end of the experiment. In Pond 4 during this second phase of the experiment, after the fish were removed the fish-food organisms showed an immediate and rapid increase in volume for two periods, followed by less rapid increase, and then after late July, by a decrease for the rest of the experiment. Similar instances of late summer decreases in fish-food biomass have been recorded previously in other ponds at this same location (Patriarche and Ball 1949, Fig. 6). In Pond 4, after removal of fish, the increase in volume of fish food came mostly from the mayflies and snails, although great proportional increases occurred with the midges, the dragonflies, and the caddisflies.

Thus the most important trends in population change of the fish-food organisms may be summarized as follows:

1. *Unidentified factors.*—Decreases in fish food occurred in both ponds in the absence of fish, revealing the existence of other major factors of population decimation.

2. *Effect of fish.*—In each pond, the fish-food biomass decreased following introduction of fish, and in Pond 4 after fish were removed there was a sharp increase in the apparent rate of growth of the fish food.

3. *Self-limiting effect.*—In both ponds, in the absence of fish, the fish-food biomass increased most rapidly at low population levels, and less rapidly later, the population eventually reaching a roughly similar upper level in each pond.

In the following paragraphs these points are first discussed in greater detail, then the quantitative relationships of these factors are explored.

1. *Unidentified factors causing decrease*

We have no quantitative information on either (1) the effect of emergence of the adult forms of certain insects, the immature forms of which are important components of the bottom fauna, or (2) other sources of mortality besides predation by fish.

Field notes record conspicuous emergences of midges early in the experiment, and of mayflies (genera *Caenis* and *Centroptilum*) during the first three weeks of August. Dates of major emergences were observed not to be identical in the two ponds but to be within a few days of one another. These observations help explain some of the population fluctuations in the absence of fish, but quantitatively emergence remains an important unknown factor.

Fish predation is obviously not the only source of mortality. Certain bottom-fauna forms such as dragonflies are predaceous, and the fluctuation in populations of non-emergent forms in the absence of fish indicates that they are subject to a considerable mortality. For example, both small and large snails practically disappeared from both ponds in August, after having been important constituents of, respectively, the fish-food and the non-fish-food bottom faunas early in the summer.

In the multiple regression analysis, the data are used for only those periods when the pond without fish showed no decrease in level of fish food. This crude adjustment to the absence of information on emergence and mortality from causes other than fish predation assumes that these factors were either constant or unimportant during periods of population increase. This is admittedly not a reasonable assumption; information on these factors would greatly increase the value of this study.

2. *Effect of fish*

That the fish had an effect upon the standing crop of bottom organisms is clear from Figure 1. When fish were in Pond 4, the fish-food biomass of the same pond was depressed well below that of Pond 5. When the fish were changed to Pond 5, the relationship soon reversed, Pond 4 now exceeding Pond 5. During the middle of the first phase of the experiment, the trend in

fish-food biomass in both ponds was upward, but at a higher rate of over-all inincrease in Pond 5 than in Pond 4. During the last half of the second phase, which was a period of great emergences of insects and mortality of other forms, the trend was downward in both ponds, but with the greater rate of decrease in Pond 5 having the fish present.

Any discussion of the rate of predation by fish on the standing crop of food inescapably involves consideration of different rates of growth, in different ponds and at different levels of fish-food biomass. Otherwise, it is difficult to understand the inability of a certain weight of fish to completely restrain the growth of fish food at a lower level, while a lesser quantity of fish immediately started to reduce the biomass of fish food at a much higher level.

3. *Self-limiting effect*

The behavior of the fish-food bottom fauna suggests that this community was self-limiting as to biomass. In each pond, roughly the same sequence of growth took place in the absence of fish—the fish-food biomass increasing rapidly at first, then less rapidly, and, perhaps by coincidence, reaching about the same upper level in the two ponds. Some self-limitation must be expected here, since a population increasing at the rate of 20 per cent per day as was that in Pond 4 in early July, would soon tie up all available nutrients and space if not otherwise checked in growth. The exact mechanics of this self-limitation are not known here; availability of nutrients, presence of waste products, and predator-prey relationships within the entire bottom fauna are obvious possibilities.

This growth behavior is consistent in general with the Pearl-Verhulst concept of logistic growth (see, among others, Odum 1953, and Andrewartha and Birch 1954). We adopt this view here as a practical device to allow some approximation of the quantitative relationships.

In general, a population (P) is said to be characterized by some maximum rate of growth (r_m). Under a particular set of environmental conditions, this maximum rate of growth is thought to be reduced proportionally as the population increases, the rate approaching zero as the population approaches some upper level (K) imposed by the environment. A common statement of this idea is,

$$\frac{dP}{dt} = r_m P\left(1 - \frac{P}{K}\right)$$

or for the (proportional) instantaneous rate of change,

$$\frac{dP}{Pdt} = r_m\left(1 - \frac{P}{K}\right) \qquad (1)$$

where t represents time.

For the quantities involved in this relationship, there are at least approximations available in the present study. For Pond 4, for example, the upper limit recorded for fish food was about 2.5 cc per square foot (or assuming a specific gravity of 1.0, about 24 pounds in the acre pond). The highest recorded instantaneous rates of growth were observed during the first half of July when an average rate of over 0.13 accompanied a fish-food biomass of about 1.0 cc per square foot.

Accordingly, from Equation (1):

$$0.13 = r_m\left(1 - \frac{1.0}{2.5}\right)$$

or

$$r_m = 0.22.$$

Such an estimate of maximum rate of growth now allows computation of the expected rate of growth at various population levels, and more important, with the fish present. The observed rates of fish-food growth with fish present did not nearly attain these calculated levels, the difference being assumed to be due to the action of the fish; this yields a clue as to the amount removed by the fish. For example, in Pond 4 during late May the fish-food level was at about 0.3 cc per square foot, a level which should have allowed a growth rate of about 0.19, but instead an average rate of increase of about 0.02 was observed. The difference ($0.19 - 0.02 = 0.17$) allows an estimate of exploitation by about 160

pounds of fish, at the rate of about 19 per cent per day. The amount actually consumed by the fish may be estimated as the product of the mean fish-food biomass and this instantaneous rate of exploitation (0.3×0.17) or 0.051 cc per square foot per day, roughly 5 pounds per day in the one-acre pond.

By this method a similar estimate might be computed for portions but not all of the experiment. During some periods the unmeasured mortality and emergence caused population declines in the pond without fish, and presumably were also of overwhelming importance in the pond with fish present. To select the data, yet avoid subjective bias as much as possible, the previously-mentioned arbitrary rule was adopted. Data from neither pond were used for a period when the pond without fish experienced a decline in fish food.

Multiple regression approach. Rather than compute a series of estimates after the manner of the previous section, a multiple linear regression solution has been used to find the most nearly consistent values. The observed instantaneous rate of change is considered the resultant of the action of several forces, all tending to reduce the growth rate below the maximum, r_m. Factors included here are the self-limiting effect of the population itself and the action of the fish. The relationship may be expressed as follows:

$$g = r_m - \frac{P(r_m)}{K} + Ff \qquad (2)$$

where:

g = observed instantaneous rate of change,

with the following constant quantities:

r_m = maximum instantaneous rate of change

K = upper limit of fish-food biomass

f = instantaneous rate of fish predation per pound of fish (carrying a negative sign),

and the following variables:

P = mean biomass of fish-food organisms

F = mean biomass of fish.

A possible danger in this approach is that it may lend a deceptive air of precision to our solution. A literal acceptance of this relationship, besides ignoring mortality and emergence, assumes exact logistic growth, predation exactly proportional both to weight of fish and biomass of prey, and constancy of the various basic rates over the several months of the experiment. On the contrary, this must be viewed as an expedient approximation.

TABLE 5. *Weight of fish and volume of fish food present in each pond at median date of each period (calculated values)*

Period (month and week)	Pond 4		Pond 5	
	Fish (lbs)	Fish food (cc/ft²)	Fish (lbs)	Fish food (cc/ft²)
April 4	138	.53		
May 1	144	.22	0	1.01
May 2	150	.24	0	1.19
May 3	155	.28	0	1.62
May 4	160	.33	0	1.86
June 1	167	.33	0	2.21
June 2	173	.35	0	2.63
June 3	180	.42	0	2.42
June 4	187	.32	0	2.19
July 1*	46	.48	41	2.39
July 2	0	1.34	144	1.99
July 3	0	2.26	147	1.62
July 4	0	2.34	150	1.39
August 1	0	2.06	152	.96
August 2	0	1.78	155	.79
August 3	0	1.21	158	.55

* Period when fish were transferred from Pond 4 to Pond 5; part of weight credited to each pond.

The selected data used to fit the regressions are shown in Tables 3 and 5. The regression has been computed separately for each pond, principally because previous work suggested that Pond 4 was inherently more productive than Pond 5. The equations, computed by standard multiple regression methods, are, for Pond 4:

$$g = 0.228 - 0.0765\,P - 0.00120\,F$$

and for Pond 5:

$$g = 0.0956 - 0.0337\,P - 0.000377\,F.$$

These equations suggest upper limits for the fish-food biomass of 3.0 cc per square foot for Pond 4, and 2.8 cc per square foot for Pond 5. There is a further suggestion that the maximum rate of increase, or potential relative productivity was greater

in Pond 4 by a factor of two, but that Pond 4 responded more rapidly to the self-limiting effect of the bottom fauna. The effect of fish was computed to be less in Pond 5, a result consistent with the lesser production of fish flesh.

The amount of food consumed by the fish during any period may be estimated as the product of four quantities: 1. per-pound effect of fish as calculated above, 2. mean weight of fish calculated to be present, 3. length of the period in days, 4. mean fish-food biomass present.

For example, in Pond 4 during the 6 days beginning May 17, the mean weight of fish present was 155 pounds. Multiplied by the calculated daily effect of one pound (-0.00120) and then by 6 days, this yields -1.12 as the instantaneous rate of fish predation on the basis of 6 days. During this period, then, the fish are calculated to have consumed the bottom fauna in an amount slightly exceeding the average standing crop (0.28 cc per square foot) or about 30 pounds of food.

A similar value has been calculated for each period when fish were in a pond. In Pond 4 during the first week of July, and in Pond 5 between cessation of sampling and removal of fish, the fish-food biomass was approximated as 0.2 cc per square foot (see Fig. 1). The total weight of food eaten by fish in each pond is thus calculated as 462 pounds in Pond 4 and 349 pounds in Pond 5.

The expected biomass growth rates of the fish-food fauna, as calculated from the multiple regression equations are shown in Table 3 for all periods of the experiment. The departures of the observed rates from those calculated may be explained, at least in part, by the otherwise unmeasured effect of insect emergence and death of part of the population as well as by sampling and measurement error. It is of particular importance that in any one period there seems to be a relationship between the two ponds in direction and magnitude of these deviations. The coefficient of correlation for the 15 paired values of these departures from calculated rates is 0.63, a value somewhat greater than expected by chance. Since the two regressions were computed separately for the two ponds, this extent of agreement within the same period of time argues for some overall influence, such as simultaneous emergence of insects from both ponds.

DISCUSSION

Among those studying the productivity of aquatic communities, it has become a commonplace that the standing crop does not necessarily reflect the productivity of a particular fauna. This point is well illustrated here, where the apparent productivity of an uncropped fauna of fish food came to a halt, with the standing crop at a high level, while a parallel fauna at a lower level was replacing itself at a high rate as it was removed by fish. This observation recalls the finding that removal of fish from a lake resulted in a somewhat higher standing crop of bottom organisms (Ball and Hayne 1952).

Under the pressure of the fish populations these ponds were capable of producing food at levels which may seem high, but which appear reasonable when the metabolic demands of the fish are considered. The rates of production of the ponds are reflected by the instantaneous rates associated with the fish predation pressure. For 150 pounds of fish, these become -0.180 for Pond 4, and -0.0566 for Pond 5, stated on the daily basis. These figures become more spectacular, and perhaps better understood if stated in different terms. In the presence of fish, the fish-food biomass produced its own volume in 5.6 days in Pond 4 and in 17.7 days in Pond 5. On the basis of a growing season of 150 days, the instantaneous rate of removal by fish becomes -27.0 for Pond 4, and -8.5 for Pond 5, implying that fish may remove in a season a quantity between 8 and 27 times as great as the average standing crop. These values are still much lower than that recorded by Allen (1951) who, working with trout in a New Zealand stream, found that on a weight basis the annual consumption of fish food was 100 times the average standing crop.

Indirect comparison may be made with

certain analyses of total productivity of bottom fauna. Miller (1941) found chironomid populations in Canadian trout lakes to be replaced 8 or 9 times a year in the shallows but only 2 or 3 times in deeper water, findings in general agreement with factors of 3 or 4 times recorded for the bottom fauna of Grosser Plöner See by Lundbeck (1926). Miller's analysis suggested that fish predation and other mortality accounted for about half the chironomid larvae in deeper water, but for relatively few in the shallows. Of the same general order are the values computed by Borutsky (1939) who found in Lake Beloie that with an average standing crop of bottom fauna of 1312.9 kg (computed by us as the average of 5 values throughout the year of Borutsky's study), the annual production was 2225.8 kg (1.7 times the standing crop) with only 542.1 kg consumed by aquatic animals (24 per cent of the production, 41 per cent of the standing crop).

All of these values computed from lakes are less than those from ponds in the present study, in spite of the fact that there is no allowance here for other predation than by fish, for natural mortality, or for emergence of adult insects. If the magnitude of the deviation of observed from computed rates of growth (in Table 3) in any way measures the importance of these other factors, then total productivity here is considerably greater than the partial value computed, and correspondingly greater than levels in the lake studies referred to above. While the greater production of fish food in these ponds may represent greater fertility of this environment, it is also possible that an important factor is more complete exploitation by the fish population.

Having information on the standing crop and growth of the fish, it is possible to test whether the previously-derived value for production of fish food may be reasonable. No measurement has been made of plant food, although it was found to make up ten per cent of the volume of food in the stomachs. Small cladocerans were also present in stomachs, and no account has been taken of their food value.

Viewed as conversion of fish food, for each pound of fish produced, there was calculated to be a consumption of 4.4 pounds of fish food in Pond 4, and 4.6 pounds in Pond 5, computed on the gross production of fish, or adding, say, ten per cent for plant and other food, about 5 pounds as an average. It is impossible here to distinguish between food required for growth and food required for maintenance of the population. These values are somewhat lower than those of Allen (1951), who found with trout that for growth alone the food required was 4.2 times the production, with an additional amount equal in weight to 1.2 per cent per day of the standing crop of fish required for maintenance in a normal population.

Ricker (1949) fed several bluegills rations of earthworms between 2 and 7 per cent daily of the body weight and observed food used to be between 6 and 11 times the growth at 20.5° C. The same author (1946) mentions several workers who have recorded in young fish of several kinds values as high as one unit of growth for three of food. Moore (1941) fed individuals of several kinds of sunfish on meat and found values between 2 and 6 times, but Ricker has pointed out that a high growth rate might be expected when using an artificial food. Our value of 5 times falls a little below those listed by Ricker.

The daily average consumption of food in this experiment may be estimated as 3.7 per cent of the fish body weight in Pond 4 and 3.9 per cent in Pond 5, averaging a little over 4 per cent when allowing for plant food. Gerking (1954) found that an average daily ration of 3 per cent of the body weight approached the maximum for captive bluegills, but Ricker (1946) quotes daily rations found by different workers as between 3 and 6 per cent of the body weight. The present values of about 4 per cent are thus within reason.

Gerking (1954) has analyzed the relationship between bluegills and their food among the bottom fauna in terms of protein. In comparing our results with his we can

only use his overall figures of 17.03 per cent protein for fish and 9.59 per cent protein for bottom organisms. On this basis our study shows a consumption of 77.8 pounds of food protein for the growth of 30.9 pounds of fish protein, with an efficiency of 40 per cent. This value is too high, judging from Gerking's results, but it would be reduced by any allowance for protein from plant or other sources. Since growth and maintenance requirements cannot be computed separately here, direct comparison cannot be made with Gerking's further work (1955a, 1955b) on protein utilization by bluegills. Those comparisons possible support the impression that the present estimates of food consumption are low.

Another view of production is in terms of energy. Totaling the production in both ponds, and allowing for no other growth, yields an average annual production of 181 pounds of fish and 811 pounds of fish food. This amount of fish is equivalent to 60.8×10^6 gram-calories per acre per year, using the value of 740 gram-calories per gram of fresh fish according to Clarke (1946). The fish food was equivalent to 331.0×10^6 gram-calories per acre per year, using conversion factors from Lindeman (1941). These values indicate an efficiency of 18 per cent in energy conversion from bottom fauna to fish, an overestimate since no allowance has been made for plant food. The total solar radiation received in southern Michigan in one year is about 431.4×10^{10} gram-calories per acre (computed from Crabb 1950). Compared to this, the fish production was 0.0014 per cent of the incident energy, and the production of fish food reached 0.0077 per cent.

Ivlev (1945) states that production of a gram of living matter requires 4000 calories. The fish growth observed here should then itself require 328.8×10^6 calories of the 331.0×10^6 consumed as food, leaving little for maintenance, and again implying that other sources of food are used.

The previous comparisons of our results with those of others suggest that our estimates of the production of fish food are a little less than adequate for a complete ration, but within reasonable range of expected values. Vegetable food, mostly *Chara*, making up 10 per cent of the diet volume, and minute crustacea in unknown quantities, may fill this energy deficiency.

CONCLUSIONS

1. In two one-acre ponds in southern Michigan, the average production of fish food by the bottom fauna during a growing season amounted to about 17 times the standing crop, when fish were present.

2. In the absence of fish, the apparent production rate of fish food organisms decreased and finally stopped at a higher level of standing crop.

3. The usual judgment, made solely from the level of standing crop, as to which of the two ponds was producing the most fish food, would have been wrong twice. The pond with the lower standing crop, and with fish present, was producing food at the higher rate in each comparison.

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Observations on Some Factors Affecting the Hatching of Eggs and the Survival of Young Shallow-Water Cisco, *Leucichthys artedi* LeSueur, in Lake Mendota, Wisconsin

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ABSTRACT

Rather suddenly, in the early 1940's, the cisco in Lake Mendota became scarce. The evidence suggested that the decline was caused by heavy summer mortalities in 1940 and 1941, but further study indicated that the summer mortalities had involved mainly older fish and that the primary cause for the decline was a scarcity of young fish in the population at the time of mortalities. Accordingly, our efforts were turned toward a search for the cause of weak year-classes, or year-class fluctuations in general.

It was postulated that year-class failures might arise if the eggs hatched under the ice because then the illumination would be insufficient to enable the larval cisco to feed. Experiments were conducted in the laboratory to determine the effects of illumination and of various patterns of incubation temperatures on the date of hatching of the eggs. Eggs exposed continuously to room illumination for 135 to 140 days hatched 7 to 8 days earlier than eggs incubated continuously in darkness. Different values of incubation temperatures acting on the eggs for about one month from the time of fertilization induced the expected proportional rates of development of eggs, but when the eggs were refrigerated at a common temperature after this first month, the rate of development of advanced embryos was retarded while the less developed embryos gained. Under such treatment, eggs incubated at temperatures differing by 1°C in the range 1°–6°C, and then incubated for the remainder of the period at a common temperature below 4°C, hatched about one day apart. Eggs incubated from the time of fertilization at a common temperature below 3°C, and then incubated for the last month at higher temperatures differing by 1°C in the range 1°–6°C, hatched 7 days apart. Eggs which had developed rapidly toward the hatching stage lay dormant for about 3 months at temperatures below 3°C. They hatched about 4 days earlier than eggs incubated continuously at temperatures below 3°C, having accumulated about 150 degree-days greater exposure. The evidence clearly indicated that the eggs of the cisco in Lake Mendota never hatch under the ice regardless of natural seasonal variations in temperatures and illumination incurred during the incubation period. Moreover, the dates of hatching are probably not affected significantly by any factor except possibly different temperatures incurred after the departure of the ice from year to year.

Experiments conducted on larval cisco indicated that they require illumination for feeding. They starve if held in darkness with natural densities of food. They begin to swallow water on the first day after hatching as indicated by keeping them in a solution of 2,3,5-triphenyltetrazolium chloride. They also begin to swallow particulate materials within the first day. By the third day they began to consume adult *Cyclops* sp. and by the fifth day better than 90% of the larval fish fed on adult *Cyclops* sp. During the first week, the swimming ability of the food organisms was a decisive factor in the degree of feeding success shown by the larval fish. The test consisted of offering living *Cyclops* sp. to one group of fish and freshly killed *Cyclops* sp. to the other group. After the first week, the fish fed equally well on both types of food.

The larval fish tolerated about 108–120 degree-days of starvation without harm. Yet, when provided with food they began to feed before the yolk sac was absorbed.

The initial postulated cause for year-class failures has been disproved. It is estimated that the eggs never hatch prior to April 25, and since 1880 the ice has not remained on Lake Mendota later than April 21.

INTRODUCTION

For almost a century, dating from the arrival of settlers, the cisco in Lake Mendota had provided continuously good fishing. Then, in the early 1940's the population declined markedly and rather suddenly. Since then it has remained at a relatively low level, a level which has yielded few rewards to the sport fishermen.

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In 1946 a study of the history of the population and its present ecology was initiated, primarily in the interest of discovering the causes for the decline and to evaluate the present position of the cisco in the community of organisms in Lake Mendota.

The present paper contains a brief account of the history of the population up to 1954, and reports on the results of investigations into some possible causes for the fluctuations in abundance of year classes.

HISTORY

The historical records compiled by Neuenschwander (1946, unpub. MS) were contained almost exclusively in the sports columns of newspapers and in the personal journals of a few interested fishermen. There had been but one ecological publication on Lake Mendota cisco (Cahn 1927) based on studies made in 1916.

Cisco fishing in Lake Mendota is done during the spawning season, a period of about two weeks beginning in late November or early December. Spawning occurs at night over depths varying between two and five meters. The cisco on the spawning grounds are relatively concentrated and readily captured by the fishermen. Prior to 1934, except for occasional changes in regulations, the fishermen were permitted to make their catches with gill nets, dip nets, or spears, lamps being customarily employed with the last two types of gear to illuminate the fish. Since 1934, the use of gill nets has been forbidden. (Apparently in Lake Mendota there have been few attempts to catch cisco on hook and line.)

From the fishermen's records only three sets of data on gill-net fishing seemed sufficiently objective to be of value in a comparison. Referring only to the largest single-night catch of a season, in 1890 between 3000 and 4000 cisco were caught using 1500 feet of net. For convenience in comparing catches, this is equivalent to 260–300 fish in a 100-foot net. In 1931 the largest single catch was 80 cisco in a 100-foot net, and in 1949 it was 28 cisco in a 175-foot net, or 16 cisco in a 100-foot net.

Catches made with dip nets and spears show the same trend as those made with gill nets. Again referring to single-night catches, in 1867 one man speared 300; in 1875, 2 men speared 875; in 1884, 2 men dipped 961; in 1938, one man dipped 214; in 1940 one man dipped 100. Between the years of 1928 and 1941 the total seasonal catches of one fisherman fluctuated between 15 and 400 fish. From 1942–1948 several seasons passed during which the fishermen not only failed to catch any cisco but also saw none. During this period the largest catch reported for the entire season was 21 fish.

Although the cisco first became noticeably scarce in the early 1940's, the population apparently started to decline around 1900. It was not possible to pinpoint the beginning of the decline nor was it possible to describe the course followed, because there were no quantitatively useful records for the interval between 1892 and 1928. The lack of records for that interval may reflect on the regulations instituted around 1900 governing the types of fishing gear that could be employed and the open season for cisco fishing. Prior to 1892 the newspapers reported on several spectacular catches of cisco. Thereafter, if such catches occurred, accounts of them were not published. Moreover, the legal fishing seasons did not necessarily correspond with the spawning season of the cisco, thus imposing unreal fluctuations in annual catches because the fishermen did not attempt to catch cisco except during the spawning season. According to the newspaper accounts, violations of the fishing season were common, but the accounts include no comments on the numbers of fish caught illegally.

Excepting the few catches made with gill nets, the records obtained prior to 1892 and after 1928 represent catches made with spears or with dip nets. Catches made with these types of gear provide an insensitive index of abundance of cisco, because the success of a fishing effort depends on the skill of the fisherman, on his ability to see the fish (a matter determined by weather conditions), and on the duration of a fishing effort. This point is supported by comparing the catches made in a fyke net against those made by one particular fisher-

TABLE 1. *The totals of fishing efforts and catches for the non-spawning seasons of 1949, 1950, and 1951*

One unit of effort is defined as a 100-foot length of net fished for one night. Fractions signify that the nets were less than 100 feet long.

Year	Size of net in inches (stretched-measure)							
	1½	2	2½	3	3½	4	4⅛	4½
1949								
Effort	¼	¼	5¾	¾		3¼		
Catch			69	13		32		
1950								
Effort	11	5½	14	13¼	13		8½	49½
Catch				9	18		13	66
1951								
Effort	3½	2¼	6½	8¾	11½	6½		7¾
Catch				4	44	29		21

TABLE 2. *Age composition of cisco in Lake Mendota represented in collections made during the years 1948–1953*

Year-class	Year of capture						Totals
	1948	1949	1950	1951	1952	1953	
1943		4	1		1		6
1944	17	90	109	83	102	25	426
1945	3	8	16	22	20	10	79
1946				1			1
1947		63	35	72	52	34	256
1948							0
1949							0
1950					2	7	9
Totals	20	165	161	178	177	76	777

man using a dip net, both fishing on the same area, the north shore of University Bay. The largest single-night catches for the seasons 1950 through 1953 were 0, 70, 3, 0 with the dip net, and 13, 41, 37, 21 with the fyke net. The 13 cisco caught in the fyke net in 1950 were taken on the first night of concentrated spawning activities during that season. Adverse weather made it necessary to take the net out of the lake on that day. It is probable that the catch would have been larger on the following nights, this having been the trend on the other years.

The historical records do not provide a measure of annual fluctuations in the abundance of cisco, but rather they indicate in broad terms the long-range trend. Even with continuous records, as for example those possessed by one fisherman for the years 1928–1941, it was not possible to interpret the fluctuations in seasonal catches.

Systematic efforts to study the population began in 1948 (Antonie 1949, Budd 1950; both unpub. MS) and continued through 1953. Except during the spawning seasons, the cisco were caught only with gill nets. The fishing efforts for 1949, 1950, and 1951 are shown in Table 1. During the spawning season of 1949 gill nets alone were used, in 1950 gill nets and fyke nets were used, and during the spawning seasons of 1951, 1952, and 1953, fyke nets were used almost exclusively. Summer fishing with gill nets was largely abandoned after 1951, because the fyke net on the spawning area captured as many cisco in a 2-week period as were captured through extensive fishing with gill nets in the summers.

The relative abundance of year-classes, based on collections made from 1948 through 1953 inclusively, is shown in Table 2.

Variations in the strength of year-classes are well defined. The occasional good year-class stands in contrast to the rather frequent occurrence of poor year-classes. The age composition of the population was not known for the years between 1942 and 1948.

During the summers of 1940 and 1941, very conspicuous mortalities of cisco had occurred. Hence, when the fishing season of 1942 proved itself a failure, it seemed obvious that the cisco population had been depleted by heavy mortalities. The explanation however is inadequate, because the fish that died during those two summers were all of a large size and probably were the older members of the population. Hasler noted that none of the specimens examined was less than 7 years old. So far as we know most of the cisco in Lake Mendota mature and spawn at the age of 3+, at the end of their fourth summer of life. Juveniles have not been captured on the spawning grounds. The poor fishing of 1942 may have been caused exclusively by the scarcity of older fish, but in the years following 1942, the scarcity of older fish was the outcome of a scarcity of immature fish in the population at the time of the mortalities in 1940 and 1941.

That the summer mortalities were not

directly the cause for the decline is also borne out in the historical records. Summer mortalities have occurred periodically in Lake Mendota as far back as the records go. The first had been observed in 1849 according to a statement in an 1867 edition of the *Wisconsin Union* (a newspaper). During the course of the present studies, summer mortalities occurred in 1953 and in 1955. The largest one on record occurred during the summer of 1932, when city officials removed an estimated 100 tons of dead cisco from the shores of the lake. Presumably mortalities have occurred annually, varying in magnitude from those discussed to those in which only an occasional carcass of a cisco was encountered. Yet, the fishermen's records (these must be viewed in the light of their subjectiveness) fail to indicate that the population, prior to 1940, had ever diminished drastically. It is noteworthy that the fishing in the late autumn of 1932 subsequent to the large summer mortality was better than it had been in the autumn of 1931. Perhaps this paradox reflects most strongly on the insensitive nature of the fishermen's catches as an index of abundance. Or perhaps it means that the recruitment of first-time spawners exceeded or balanced the losses caused by mortalities.

In one respect, the records for Lake Mendota are surprisingly uniform: the summer mortalities always comprised only large fish. The same applies to other lakes where summer mortalities of cisco commonly occur (Cahn 1927; Wisc. Cons. Dept., per. comm.). Frey (1955) has reviewed similar evidence on American, European and Russian coregonids. The victims examined from Lake Mendota during 1941 were not less than 7 years old, and those of 1953 were 9 years old, but the fish that died in 1955 were 3 to 10 years old. The records so far indicate that cisco less than 3 years old have not been involved in summer mortalities.

Presumably the fish that died during most summer mortalities would have spawned between three to five times prior to their death and, therefore, should have contributed substantially to the perpetuation of the population, had there been any appreciable survival of their eggs and offspring. Fundamentally, it would seem that the decline in Lake Mendota in the early 1940's and the persistent low level of the ensuing population have resulted from reproductive failures.

SUSPECTED CAUSE OF YEAR-CLASS FAILURES

The literature on the cisco and on whitefishes in general pertaining to fluctuations in the strength of year-classes suggested several plausible explanations for the fluctuations in Lake Mendota. The most interesting possibility and the one attracting immediate attention is that the survival rate of year-classes might be determined by circumstances related to the time of departure of the ice in spring. Einsele (1941) working on the whitefishes of some Austrian alpine lakes, postulated that weak year-classes arose through heavy mortalities caused by starvation of the larval fish when the eggs hatched under the ice, particularly during late springs when the departure of the ice was substantially delayed. The starvation, according to his observation, was brought on by the combined adversities of a scarcity of food organisms (zooplankton), and insufficient illumination to enable the larvae to see and capture these organisms. When the ice departed at earlier dates, the larvae were not subjected to these conditions.

Cahn (1927) estimated on the basis of eggs dredged from the lake that the cisco in Lake Mendota hatched in the latter half of March. If this estimate were correct, it seemed possible that Einsele's theory might have application in explaining the fluctuations in year-classes in Lake Mendota. The date of departure of the ice in recent years has varied from March 20 to April 16. In view of Cahn's estimate, on some years the eggs would have hatched several days before the departure of the ice, which could have set the stage for the emergence of poor year-classes.

Initially, the problem was to find out whether or not a correlation existed between the dates of hatching relative to the dates of departure of the ice, and the strength of year classes represented in the collections made

between 1948 and 1953. In order to obtain estimates on the dates of hatching for past years, it was necessary to consider the annual variations in factors that might correlate with the hatching dates, e.g., the time of spawning and the patterns of water temperatures and solar illumination during the period of incubation.

Although there are other physical factors that might influence the dates of hatching, only temperature and illumination were investigated. The general relationships between temperature and dates of hatching have long been known. The relationships between illumination and hatching dates were not clearly understood, but studies on other fishes (Dannevig 1932, McHugh 1954, Steinmann 1950, Vibert 1953, and Wagler 1941) suggested that illumination might have a significant effect on the hatching date.

So far as is known, the cisco in Lake Mendota complete spawning no later than December 15 regardless of the temperature of the water. In 1953 the spawning began when the temperature of the lake was 5.4°C and ended when the temperature stood at 4.6°C (John 1956). Generally, the fish begin to spawn after the temperature falls below 4°C, which usually happens between the third week of November and the first week of December. In 1955 ripe females were captured the day before the freeze-up and most likely would have spawned after ice had formed. The temperature was 2.5°C. Fyke nets set on the spawning area of University Bay provided the data on the terminal dates of the spawning activities.

The lake usually freezes over within 20 days after the completion of spawning, but there is no consistent correlation between the two events. An early spawning season is not necessarily followed by an early freeze-over.

During this pre-freeze-over interval of open water, the eggs are subjected to rather striking differences in the sums of temperature-degree days from one year to the next. This is one variable in the incubation pattern. Following the freeze-over, they must endure a prolonged period of lower temperatures. Secondly, the eggs are subjected to different values of temperature at different times during their later stages of incubation; the temperature of the water under the ice may begin to rise on different dates from year to year, may rise at different rates and may reach different values. Finally, the amount of solar illumination reaching the eggs varies considerably from season to season. Primarly these variations are dependent on the duration of open water following the spawning season, the thickness of the ice and snow, and the pattern of solar radiation.

INFLUENCE OF LIGHT AND TEMPERATURE ON HATCHING

General procedures

During the four seasons 1950–51, 1951–52, 1952–53, and 1953–54, eggs obtained from the cisco in Lake Mendota were stripped from the females into a dry pan and fertilized by the sperm from two or three males. About a minute after fertilization the eggs were treated with a thick aqueous suspension of soil particles to eliminate their cohesive or adhesive properties. After washing away the excess soil, the eggs were transferred to hatchery incubation jars in which they were kept in constant "rolling" motion, or to screen-bottomed trays floating in water baths. The eggs from all females were intermixed to assure an approximately uniform composition of all lots. The hatchery jars had a capacity of about 6 liters and were supplied with water at an average rate of 2 liters per minute.

At all times, except for some experiments conducted during the 1953–54 season in which the water was a mixture from Lake Mendota and city artesian wells, the water was obtained via the University Pumping Station from Lake Mendota. The intake lay 15 feet below the surface and about 200 feet from shore. Temperatures higher than that of the lake water were obtained either by mixing warmer artesian water with the lake water or by setting the container of eggs in a temperature-controlled water bath. Temperatures were determined daily to the nearest tenth of a degree with an ordinary 110°C-thermometer. The temperature in

the hatchery jars was always about 1°C higher than that in the lake, at the depths occupied by the eggs.

The dates of hatching represent the time at which half the eggs in a particular lot had hatched. In the hatching jars, containing from 40–60,000 eggs, the time at which half the eggs had hatched was estimated. In the trays, it was determined by keeping a cumulative record of the daily hatch.

The influence of illumination on dates of hatching was studied by incubating one group of eggs in the dark and a similar group in the light. Several experiments were initiated to determine the relationships between the dates of hatching and various patterns of incubation temperatures: eggs were subjected to different temperatures only during the early stages of development and thereafter were incubated at a common low temperature. Other eggs were incubated at unusually high temperatures to hasten the rate of development and were then held for the remainder of the time at a much lower temperature. Eggs incubated at low temperatures were placed at still lower temperatures just prior to their expected time of hatching. And eggs incubated at a common low temperature were incubated at different higher temperatures during the last stages of the incubation period.

General observations

During the four seasons of these studies, eggs incubated continuously at the lowest temperatures available in water delivered from the University Pumping Station hatched after or shortly before the departure of the ice (Table 3). Although the dates of hatching varied only slightly, there were appreciable variations in the dates of fertilization, and the dates of formation and departure of the ice on the lake. The thermal patterns for the four seasons are not given, but the two extremes are shown in Figure 1.

The eggs incubated in hatchery jars hatched in small numbers for about six weeks preceding the main hatch, and the larval fish were carried upward and out of the jar by the currents of water. Hence, one could be certain when observing the larvae that they had not been drifting in the jar for any appreciable length of time. During the first week or so of this period of early hatching the larval fish observed in the jar were dead. Perhaps they had not hatched but had died and were released when the capsule of the egg deteriorated. During the remainder of this period the majority of the larvae were alive, but by comparison to those that hatched later, they were premature. They were smaller, less pigmented, and possessed relatively large oval yolk sacs, all of which are features of prematurity. However, these premature larvae were successfully reared to the fry stage.

The onset of premature hatching was inversely proportional to the incubation temperature.

The early hatching was in part abnormal due to mechanical agitation produced by the continuous "rolling" motion of the eggs in the hatchery jars. When kept in a tray floating in a calm water bath, eggs that are ready to hatch can be induced to hatch

TABLE 3. *Dates of fertilization and hatching, and dates of formation or "freeze-up" and departure or "break-up" of ice during four-year period of study*

Fertilization	Freeze-up	Break-up	Hatching	Incubation (days)
Dec. 2, 1950	12–11–50	4–11–51	4–7–51	127
Nov. 28, 1951	12–12–51	4–12–52	4–9–52	132
Dec. 4, 1952	12–25–52	3–21–53	4–8–53	126
Dec. 12, 1953	12–30–53	3–25–54	4–10–54	120

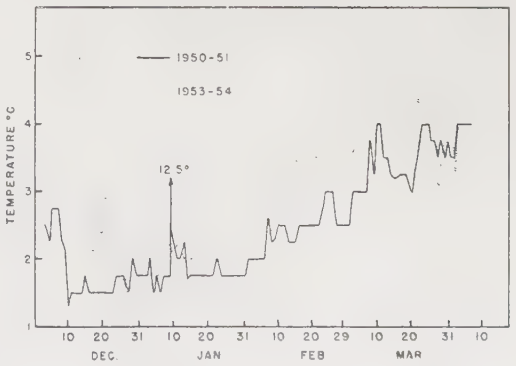

FIG. 1. The two extreme patterns of incubation temperatures encountered during the four-year period 1950–54. Temperatures were taken in the hatchery jars.

almost instantly by agitating the tray for a moment. When not disturbed, the eggs remain unhatched for several additional days. Price (1940) stated that agitation caused an early hatch of eggs of *Coregonus clupeaformis*. The early hatch of the cisco apparently was caued by the activities of the embryos within the eggs. These activities were, in turn, induced by the mechanical agitation. Further evidence to support this view is discussed under the experiment on the effects of illumination on hatching.

Early hatching in the jars might have been partly normal. Small numbers of eggs in the jars continued to hatch for a few days after the main hatch. One lot of 200 eggs maintained in a relatively unagitated tray at a temperature of 6°C hatched over a period of 25 days. Therefore, one might normally expect hatching to occur in the jars over a relatively long interval of time, especially since the temperatures were lower than 4°C. Embody (1934) stated that the eggs taken from a single female trout hatched over a period of 15–20 days at low temperatures (values not given), the span decreasing with increasing temperature. It appears that one effect of agitation would be to shift the entire hatching interval downward on a time scale.

It is noteworthy that in spite of continuous premature hatching, there was no difficulty in estimating the peak of hatching activities. Most of the eggs hatched within a period of 3 to 4 days.

There are no data on the hatching sequence of unagitated cisco eggs at temperatures below 4°C.

Effects of illumination on hatching

Methods. During the seasons of 1951–52 and 1952–53, two jars of eggs were incubated continuously in light-tight boxes finished with asphaltum on the interior and with aluminum paint on the exterior. Two control jars were subjected to continuous illumination, a mixture of artificial and natural light, the latter entering through windows. During the first week, the critical period in adjusting the flow of water through the jars, the boxes were opened frequently but briefly. Thereafter, they were opened about once a week until the controls had begun to hatch, after which they were opened daily in order to establish the date of hatching. From the time that the eyes became pigmented until the controls hatched, samples from the two sets were transferred periodically to screen-bottomed trays floated in a container of water and exposed to continuous room illumination. The temperature of the water in the container at the time of the transfer was the same as that in the hatchery jars. It increased within a few hours, and remained at room temperatures of 17–20°C until the eggs hatched.

Results. The eggs subjected to continuous illumination hatched seven days earlier than those held in darkness in the 1951–52 trial and eight days earlier in the 1952–53 trial. The eyes of the embryos in the dark became pigmented at the same time as those in the light. Samples of eggs removed periodically from the illuminated and non-illuminated jars and thereafter incubated in the same water bath at room temperatures always hatched within the same day. Toward the end of the experiment, among the samples incubated at room temperatures, the eggs that had been held in continuous illumination hatched a few hours before those that had been held in darkness.

The temperatures of the water issuing from the illuminated jars were the same as those for the non-illuminated jars, to the nearest hundredth of a degree, determined with a Whitney resistance thermometer. During the extension of seven to eight days in their incubation time, the eggs in darkness accumulated some 30–40 degree-days in excess of the sums acquired by the illuminated eggs.

Response of early embryos to different temperatures

Methods. Eggs were incubated at different temperatures for about one month and then were incubated at the lower temperature for the remainder of the period. Three lots (4, 5, 6) were used and were treated as follows: from December 12,

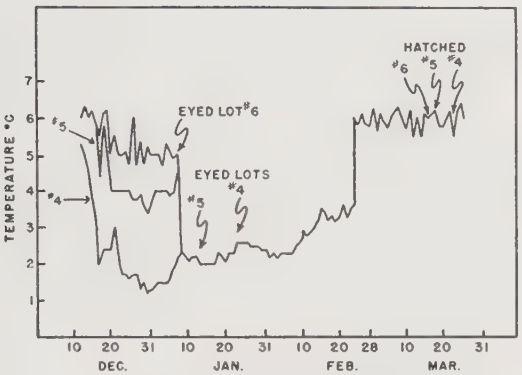

FIG. 2. Thermal histories of eggs subjected to different temperatures only during the early part of the incubation period.

date of fertilization, to January 9, Lot 4 was incubated at a mean temperature of 2.3°C, Lot 5 at a mean of 4.5°C, and Lot 6 at a mean of 5.4°C. Subsequent to January 9, all lots were incubated at a common temperature (below 3.5°C) until February 24. On February 24 the temperature for all lots was raised to 6°C in order to decrease the variations about the mean dates of hatching. The dates on which the eyes of the embryos became pigmented ("eyed-stage") were used as reference points against the dates of hatching.

Results. The eyes became pigmented in 27, 33, and 43 days after fertilization, differences of 6 and 16 days (Fig. 2). In the same order, the lots required 96, 98, and 103 days to hatch, differences of 2 and 7 days. The advantage in development shown by eggs incubated earlier at higher temperatures was substantially reduced during the following period of incubation at lower temperatures. Held for 25 days at temperatures differing by 1°C, in the range of 1°–6°C, and then incubated at a common temperature, the lots hatched about 2 days apart.

Effect of refrigeration on artificially advanced embryos

Methods. Eggs fertilized on November 28 were incubated in a hatchery jar at temperatures below 4°C until December 5, at which time a sample of about 2000 was taken from the jar and incubated at temperatures that varied from 7–12°C up to December 17, and from 5–10°C up to January 6. On January 6 when the eggs appeared to be nearing the hatching stage the sample was divided into approximately equal lots: one lot was held at room temperatures, 17–20°C, the other was placed in a screen-bottomed tray in a water bath of the same temperature as the water flowing through the hatchery jar.

Results. The lot held at room temperatures after January 6 hatched on January 12, 13, and 14. The other lot, incubated after January 6 at the lower temperatures of 1.5–3.0°C, hatched in the following sequence:

Date	Number Hatched	Date	Number Hatched
Jan. 14	4	Mar. 2–15	2/day (estimated)
Feb. 21	7	Mar. 16–31	8/day (estimated)
22	5	Apr. 3	50
25	8	4	190
27	3	5	65
28	8	6	22
Mar. 1	21	7	some eggs still unhatched

On December 15 the eyes became pigmented in the eggs subjected to higher temperatures. Those in the hatchery jar became pigmented on January 3. The peak of hatching activities in the jar occurred on April 7–10, and in the experimental lot, as shown above, on April 3–6. The difference of 19 days in the appearance of pigment in the eyes of the two lots was reduced to about 4 days in the dates of hatching. As a conservative estimate, those that had been subjected to higher temperatures accumulated between 130 and 150 degree-days in excess of those incubated in the hatchery jar. The embryos that had appeared to be about fully developed on January 6 had lain essentially dormant for 3 months.

The larvae that hatched before March 1 were for the most part abnormal in their behavior and external appearance. Their bodies were either permanently bent, or, if they looked physically normal, the larvae swam in circular or corkscrew paths. Those that hatched after March 1 appeared to be well-developed and behaved normally.

The hatching activities of the lot subjected to higher temperatures extended from January 14 to and beyond April 7. The first observed hatching in the jar occurred on March 2, and the eggs had almost completely hatched by April 12. The early hatching, particularly in the jars that had received water of the lowest available temperatures, seemed abnormal. The fry observed on March 2 and for several days thereafter were definitely premature in their appearance and were dead when observed. Later on, though still premature in appearance, they were alive and could be reared beyond the larval stage. It is likely that the "rolling" activity in the jars contributed to the premature hatching. Although the eggs in the experimental lot were not so vigorously agitated between January 6 and April 7 as those in the hatching jar, they were kept in more or less constant motion by the circulation in the water bath, and some of the early hatching might have been induced by this motion.

Refrigeration of late, normal embryos

Methods. On March 21, 1953, eggs that were incubated at temperatures below 4°C from the time of fertilization on December 4, 1952, were transferred to finger bowls and kept in a refrigerator at a temperature of 2 ± 1°C to find out if the incubation period might be extended by exposing the eggs to lower temperatures during the late stages of development. Such conditions might be caused naturally by a change in the weather or by the ice remaining on the lake until the early part of May.

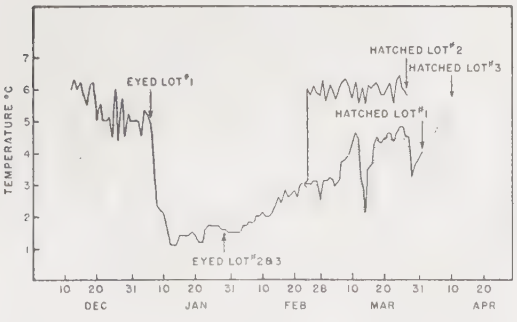

FIG. 3. Thermal histories of eggs subjected to different temperatures only during the late stages of incubation. The record for Lot 1 has been included to illustrate the differences effected by temperatures during the late period as opposed to the early period.

Results. The eggs in the refrigerator hatched continuously in small numbers. It is noteworthy that some remained unhatched as late as May 8. These hatched when they were removed from the refrigerator and exposed to room temperatures. The eggs in the hatchery jar from which the samples had been taken hatched completely by April 14.

Response of late embryos to different temperatures

Methods. Two lots of eggs (No. 2, 3) were incubated from the time of fertilization, December 12, at a common temperature until February 24 when the embryos had reached an advanced stage of development, and then were incubated at different higher temperatures, Lot 2 at a mean of about 6°C and Lot 3 at a mean of about 4°C.

Results. Lot 2 hatched about 14 days earlier than Lot 3, indicating that a 1-degree difference acting through a period of about one month during the late stages, produces a 7-day difference in dates of hatching (Fig. 3).

The data for Lot 1 have been included in Figure 2 to illustrate the greater shortening of the incubation period induced by higher temperatures during the late stages of the period in comparison to those afforded a similar exposure during the early stages. The fact that Lot 2 with a total of 324.3 degree days hatched on March 27, whereas Lot 1 with the greater total of 345.5 remained unhatched (it hatched five days later) indicates that the additional thermal units afforded Lot 1 by the higher temperature prior to January 11 were not effectively used in the early developmental processes. The temperature apparently exceeded the optimum.

There was a smaller difference between the temperatures of Lots 1 and 2 after February 24 than there was prior to January 11, though the durations of exposures were nearly equal. Prior to January 11 Lot 2 had been incubated at lower temperatures than had Lot 1 subsequent to February 24.

It is not unlikely that the hatching of Lot 1 would have been further delayed had the temperature been a degree or so lower.

It seems not unreasonable to suspect that the higher temperature acting on Lot 2 after February 24 may have hastened the hatching not simply through speeding up maturation processes, but also by stimulating the activity of the embryos and giving rise to a mechanical rupture of the egg capsules. However, this latter mechanism appears not to have been important. A sample of eggs from Lot 1 were incubated with Lot 2 at the higher temperature subsequent to February 24. They hatched on March 17, 10 days earlier than did Lot 2. This is essentially equivalent to the 9-day difference obtained between Lot 1 and Lot 3, both of which were incubated at a common temperature after February 24.

Attempts were made to incubate the eggs in the lake within the range of depths at which they are thought to be deposited naturally. In the fall of 1951, and again in 1952, immediately after fertilization, eggs held in screened boxes were placed in the lake. As a result of damage to containers wrought by unforeseen storms the efforts were largely unsuccessful. On April 2, 1952, 14 eggs fertilized in the fall of 1951 were recovered from the salvaged fragments of one of the boxes. By comparison to those in the laboratory, the embryos were considerably retarded in their development. Not only were they smaller but they also were less pigmented and possessed relatively large oval yolk sacs.

ON THE FEEDING BEHAVIOR OF NEWLY-HATCHED CISCO

General materials and procedures

Larval fish, taken on the day on which they hatched, were subjected to the experimental conditions to determine: 1) whether or not they require illumination to feed, 2) how long they can endure starvation, 3) when they begin to feed and the quality of the food eaten, and 4) the relationship between their feeding success and the ability of the food organisms to escape. Care was taken to select only the apparently healthy and normal individuals in order to minimize the ambiguity of the results, for in all the experiments the end point was based on whether or not the fish contained food in their digestive tract, an end point which would convey misinformation if the fish in question were incapable of feeding for reasons aside from those intended in the experiments. For the most part, by virtue of the transparency of the larvae, the occurrence of materials in their digestive tract was obvious to the naked eye. Only in experiments making use of particles of carbon, in which the particles were camouflaged by the melanophores of the peritoneum, was it necessary to remove the digestive tract for a decisive determination of the results.

Most of the experiments were carried out at the temperatures encountered in the aquarium room, 14°–18°C. In those experiments where temperatures were known to have an important bearing on the results the values are given.

Dependence of feeding on illumination

Methods. To determine whether or not the larval fish feed during prolonged darkness, they were confined at the time of hatching to aquaria held in darkness.

Equal numbers of larvae placed in adequately illuminated aquaria served as controls. The aquaria were supplied with an abundance of food organisms, principally species of *Cyclops* and *Diaptomus*. About 4 days after the fish in the controls began to eat, the fish were removed from the darkened aquaria and examined individually for signs of feeding activity. Additional tests were made, using inanimate materials such as particles of carbon and carmine, to find out if the procurement of food in the dark depended on the density of food available.

Results. Deprived of illumination, larval cisco apparently are unable to capture living zooplankters (Table 4). But the results in these tests were not without inconsistencies. A rather substantial number in the third set from the dark contained at least one food organisms in their digestive tract, but none contained more than three. In contrast, those from the control possessed, for the most part, full digestive tracts, the capacity

TABLE 4. *Feeding success of two groups of larval cisco: one group fed in darkness, the other fed under adequate illumination*

Food was living zooplankton, mainly *Cyclops* sp.

Date	Age at start (hours)	Age at end (days)	Fish in dark			Fish in light		
			Number at start	Survivors	Number eating	Number at start	Survivors	Number eating
4–7–51	24	7	100	56	5	100	36	32
4–11–51	24–96	11–14	100	29	0	100	27	27
3–8–52	24–48	7–8	200	193	32	200	196	151
3–15–52	0–24	11	200	195	3	200	189	142

being approximately 7 to 10 full-grown *Cyclops*. Apparently the fish in the dark managed to catch a few food organisms because the food was supplied in excessive quantities. Approximately equal amounts of plankton were added to the containers each day, but it was not possible to control the numbers in the dark without admitting light. Perhaps the food was so dense that by chance alone a fish occasionally encountered a plankter, or perhaps the fish succeeded in finding dead plankters which offered no resistance to being consumed. In the series of tests in which the larvae were offered copious quantities of particulate carbon and carmine, the fish in darkness consumed the particles to about the same extent as those in the light (Table 5).

When the fish are provided with lower concentrations of living food (20 to 40 organisms per liter) they must be able to see the individual organisms for they often expend considerable time in pursuit before succeeding in catching a plankter. In fact, the frequency of successful pursuits in the first days is so low as to give rise to a suspicion that the larvae are unable to catch healthy zooplankters. The larval fish did feed occasionally on dead organisms lying on the bottom of the aquarium, but tests in which large numbers of dead organisms lay on the bottom indicated that the habit was not sufficiently common to alter the results materially.

TABLE 5. *Consumption of particulate materials by larval cisco in darkness and under room illumination*

Duration of tests was 6 to 10 days.

Number of fry at start	Illumination		Without illumination	
	Survivors	Number eating	Survivors	Number eating
Carmine particles				
60	20	18	17	13
30	25	8	29	17
Carbon particles				
60	52	16	52	25

The causes for the low numbers of survivors in the 1951 experiments (Table 4) were unknown. Nor was there an explanation for the rather consistent failure of the survivors under illumination to have achieved a 100 per cent success in obtaining food. Possibly the end point based on whether or not the larvae contained food in their digestive tract was deceiving. Other observations showed that the zooplankters may pass completely through the digestive tract within 24 hours.

Capacity to endure starvation

Methods. The capacity of the larvae to endure starvation was determined at the temperatures that they might encounter naturally after the departure of the ice. The experiment was initiated on April 8, 1952, 3 days before the ice disappeared. Forty larvae were placed in each of 26 three-liter containers (duplicate sets of 13) filled with cotton-filtered lake water, and set in a bath of running lake water. After a lapse of 8 days living zooplankton was added to the first two containers and thereafter, at 2-day intervals, it was added to subsequent sets. The food was maintained at a substantially high level for a period of 7 days for each set of containers. At the end of 7 days the fish were removed and examined for signs of feeding activity. The daily mortalities in each jar were recorded.

Results. Detailed results of the experiment are given in Table 6. The thermal history for each lot is expressed as the sum of degree-days, thus giving a measure of the physiological age of the individuals. The temperature at the beginning was 4°C and rose rather steadily to 11°C during the 32-day course of the experiment. During the first 22 days, among the starving fish

TABLE 6. *Larval cisco subjected to starvation from time of hatching, then offered live zooplankton for a period of seven days*

Forty fish in each lot at beginning of experiment.

Lot	Starvation			Days (starvation plus seven)	After Feeding		
	Days	Degree-days	Survivors		Survivors	Number eating	Per cent eating
1	8	41.9	40	15	28	27	96.3
2			40		5	5	100.0
3	10	53.3	40	17	37	31	83.7
4			40		26	24	92.3
5	12	65.5	40	19	34	31	91.1
6			40		38	28	73.6
7	14	79.5	40	21	35	23	65.7
8			40		38	32	84.2
9	16	94.0	40	23	38	36	94.7
10			38		34	32	94.1
11	18	108.0	40	25	37	36	97.3
12			40		36	36	100.0
13	20	128.0	40	27	34	21	61.7
14			40		34	16	47.1
15	22	149.5	40	29	6	6	100.0
16			39		13	13	100.0
17	24	174.8	25	31	0	0	
18			24		0	0	
19	26	200.3	10	33	0	0	
20			11		0	0	
21	28	231.3	4	35	0	0	
22			9		0	0	
23	30		0				
24			5				
25	32		0				
26			0				

there were essentially no mortalities (Table 7). On day 23 mortalities occurred in all the lots and the peak rate of mortalities fell on day 24. Thereafter, mortalities continued rather uniformly in all lots. Once the starved fish had begun to die, there were no survivors among them at the end of the 7-day feeding period.

Considering only the higher values of survival from each set of jars (Fig. 4), it appears that the larvae tolerated 18 days (108 degree-days) of starvation after hatching without ill effects. Although 100 per cent of the larvae survived through 22 days of starvation, after 18 days some had apparently become too weakened to take advantage of the food made available to them. But the exact breaking point in the curve may be obscured by other factors. It is possible that the survivors decreased on day 18 because of disease or accidents. Unquestionably, the poor survival in Lot 2 was not caused by starvation. It is significant that the survivors were consistently

TABLE 7. *Mortality statistics for larval cisco starved from time of hatching*

Thermal age of fish same as in Table 6.

Days of starvation	Average mortality per jar	Standard deviation	Number of jars in average
8			26
9			24
10	0.08		24
11			22
12			22
13			20
14	0.05		20
15			18
16	0.05		18
17			16
18			16
19			14
20	0.15	0.35	14
21	0.9	1.47	12
22	0.8	1.10	12
23	2.8	2.31	10
24	6.5	3.02	10
25	5.5	4.47	8
26	5.0	2.95	8
27	2.2	2.48	6
28	2.0	1.54	6
29	3.5	2.57	4

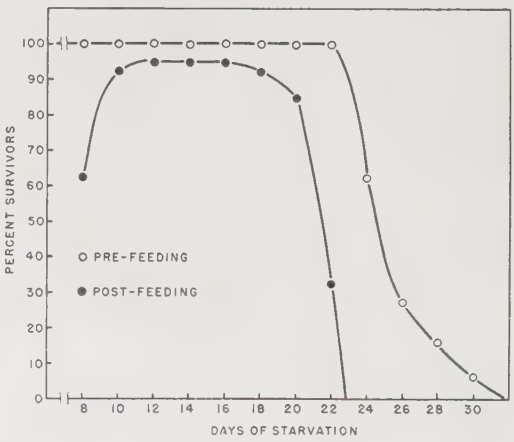

FIG. 4. Survival of starved larval cisco, and the survival of the same larval cisco after a seven-day period of feeding. The age of the fish represented by the post-feeding curve is days of starvation plus seven.

fewer after feeding than before feeding, even considering the lots in which the fish were less than 22 days old, their age being starvation time plus 7 days of feeding time. One observation indicates that these mortalities were, in part, caused by accidents. Shortly after introducing food to one lot, one fish began to swim in a convulsive manner and soon settled to the bottom of the jar. An examination of the fish under a dissecting microscope showed that a small *Daphnia* had become lodged between the gills and the operculum on one side.

The end point in this experiment, however, was not based solely on the numbers that survived the 7-day feeding period, but also on the percentages of these survivors that had eaten. This latter attribute varied appreciably (Table 6), yet on day 22, the last day of any survivors among the fish that had been fed, 100 per cent contained items of food. Considering both the survivors and the percentages that had eaten, the maximum survival seems to persist only to day 18. Prior to this the percentages that had eaten were not uniformly high. As mentioned in connection with the studies on the procurement of food by larval fish confined to darkness, the end point may have been ambiguous. The absence of food in the alimentary tract does not prove either that the fish had not eaten, or that they would not have eaten in the future. However, when provided with adequate food, once the larvae began to feed they generally fed persistently.

In the range of temperatures encountered, it appeared that the larvae could endure between 108–128 degree-days of fasting; no fatalities ensued. At lower temperatures, such as those encountered under a cover of ice, they could survive much longer. Starved for 29 and 34 days at temperatures between 3°–4°C, 100 per cent of the larval fish fed successfully when they were given living zooplankton.

Time of first feeding

Methods. The time at which the larvae first feed (or swallow water) and the success of their feeding efforts in relation to their age were determined with a variety of materials: a water solution of the enzyme-activity indicator 2,3,5-triphenyltetrazolium chloride (T.P.A.); particles of carmine and carbon; eggs of zooplankters; and living zooplankton. The duration of the tests varied as did the numbers of larval fishes employed. Three groups of larvae were placed in a solution of T.P.A. at the time of hatching and remained in the solution for 12, 30, and 48 hours. One hundred larvae (about a day old) were fed on eggs of zooplankton for one hour. At the time of hatching about 200 larvae were placed in a 20-gallon aquarium well supplied with living zooplankton. Each day 10 larvae that appeared to be feeding actively were removed, examined for food contents, and preserved in formalin. Similar procedures were used on the larvae that were fed particulate carbon and carmine except that the larvae were confined to 3-liter jars. Prior to the time of testing, if the larvae were not newly hatched they had been kept in cotton-filtered lake water deprived of any source of food.

Results. The larvae demonstrated their first signs of feeding behavior within a few minutes after hatching. Though swimming vigorously and rather continuously for the most part, they paused periodically to fix their attention on plankters, air bubbles, or other particles. Not infrequently they stopped swimming and, head foremost, glided downward, generally recovering before reaching the bottom, to take off on another burst of rapid, continuous activity. Within the first day they abandoned this ritual of periodic nose-dives, and thenceforth appeared to swim continuously, never resting until they had outgrown the larval stage and had acquired the general form and appearance of miniature adults. During the first day they began to swallow water, as indicated by the orange color in their digestive tract produced by 2,3,5-triphenyltetrazolium chloride; the containers were free of particulate matter. Also, during the first day they began to feed on eggs of the planktonic crustaceans.

Between day 1 and 2 they began to consume particulate carbon, and after day 2 they consumed particulate carmine. The

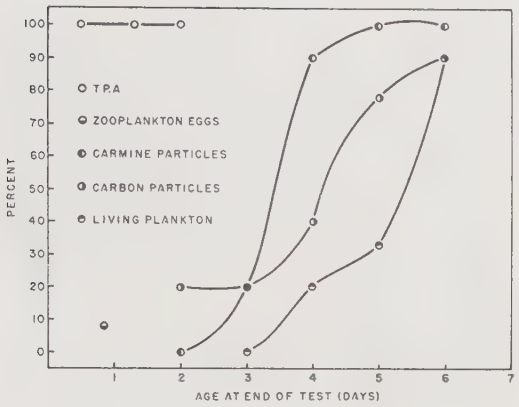

FIG. 5. The age-feeding relationships of larval cisco. Abscissa shows age of larvae at end of test. Ordinate shows per cent of larvae that had eaten the materials. T.P.A. is 2,3,5-triphenyltetrazolium chloride. Zero point for carbon has not been determined.

exact age at which the larval fish began to feed on these particulate inanimate materials is not known. An occasional fish consumed particulate carbon within the first day of hatching. Around the third day a few individuals had begun to feed on living zooplankton, the numbers increasing rather rapidly thereafter to a maximum by the fifth or sixth day. The curves in Figure 5 suggest the manner of change in their feeding. It is noteworthy that the larval fish within three days after hatching consumed adult *Cyclops* or *Daphnia* of an equivalent size. In addition to the materials mentioned the larval fish consumed small clusters of blue-green algae, minced beef liver, and air bubbles. The fish that swallowed air bubbles soon died because the bubbles held them in an upside-down position at the surface of the water. The bubbles were inescapably lodged in the intestine.

Ability to capture food

Methods. A relationship between the feeding success of the larvae and the agility of the food organisms was established by feeding living zooplankton to one group and freshly killed zooplankton to the other. The duration of each test was one hour. Either 100 or 200 larvae were placed in each of two four-gallon battery jars containing cotton-filtered lake water. The food organisms, predominantly *Cyclops* sp. of quite uniform size, were obtained by washing a collection of plankton through a graded series of bolting cloth sieves (7, 9, 15, 21, and 26 meshes per linear centimeter). Those collected on the 26-mesh sieve were used in the study. To minimize the numbers of dead or injured plankters in the final preparation of living food, the collection was allowed to settle in a separatory funnel and the sediments were drawn out and discarded. Organisms for use as dead food were killed immediately before each test by immersing them in boiling water. The dead organisms were kept in suspension by currents generated with an aeration nozzle, and currents were similarly generated in the other container. Observations also were made on the ability of the larvae to capture different species of living zooplankton.

Results. During the first week the success and efficiency of the larval fish in capturing food organisms depended rather strongly on the swimming ability of the organisms. Thereafter, the differences became negligible, at least insofar as *Cyclops* sp. was concerned, as was shown by comparison of the fish's success in feeding on living and dead *Cyclops* (Fig. 6). The results give a measure only of the numbers of fish that had eaten at least one organism during a one-hour period, whereas the efficiencies based on the average numbers of organisms eaten by the fish stand much farther apart. The larvae provided with living organisms had eaten between 1 and 3 individuals; the majority of those provided with dead organisms had eaten between 3 and 7.

The results of Figure 6 regarding the time of consumption of living zooplankton are not strictly comparable to those of Figure 5. In Figure 5 the fish first contained zooplankton after the third day. In Figure 6 they contained zooplankton on the second day. It is thought that this difference might best be ascribed to the different procedures employed. For the results in Figure 5, 10 active fish were removed from the aquarium each day and examined for food content. Those that had eaten avoided capture. General observations on the stock sampled

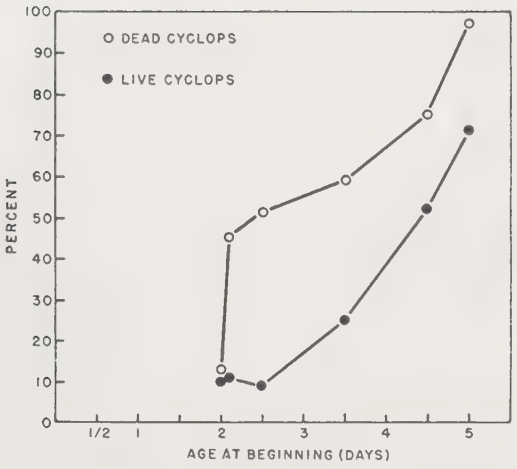

FIG. 6. The success of feeding by larval cisco as measured by the motility of the food organisms. Abscissa indicates age of larvae at beginning of test. Ordinate indicates per cent of larvae that had eaten. Duration of each trial was 1 hour. Each point is based upon either 100 or 200 fish. Curves have not been drawn to zero. Up to and including day 1½, none of the fish fed during the one-hour test.

revealed that some were eating before the third day. The assumption that 10 fish would represent the stock in the aquarium was obviously unjustified. For the results in Figure 6, each test conducted on days ½, 1, etc., employed at least 100 fish. Presumably Figure 6 more nearly represents the true feeding pattern so far as living *Cyclops* are concerned.

Observations on the success of the larval fish in capturing various living organisms also showed that the swimming ability of the food organisms is a decisive factor. For example, though the size of the organisms and their abundance were not limiting factors, *Diaptomus* was seldom eaten whereas *Cyclops* made up the principal part of the diet. In observing the larvae in pursuit of these two organisms, one harbored little doubt that the scarcity of *Diaptomus* in the diet as compared with *Cyclops* could be attributed to the greater swimming ability of the former. A similar conclusion was reached by comparing the relative difficulty of capturing these organisms with an eye-dropper.

The larval fish began to feed before the yolk sac was absorbed. At temperatures ranging between 14–18°C, the yolk sac had completely disappeared by the sixth day. It is noteworthy that the fish tolerated at least 10 days of starvation at these temperatures.

The preceding results have pertained only to larval fish at the time of hatching. Within two to three weeks after hatching, at temperatures between 14–18°C, the larvae acquire the general form and appearance of miniature adults, their length varying between 16 and 20 mm. From this stage onward they feed on any organism small enough to be swallowed, whether it be encountered in suspension (the typical position of planktonic crustaceans), at the surface (as was the case with adult midges), or on the bottom (the source of midge larvae). It was of interest that "early-hatch" cisco, which were between 20–50 mm in length by April, voraciously consumed newly hatched larval cisco.

SIGNIFICANCE

The decrease of 7 to 8 days in the incubation period of eggs subjected to continuous illumination compared with those incubated in essentially continuous darkness seems particularly significant in view of the fact that those in darkness accumulated an additional 30–40 degree-days during the 7–8 day period. It might be suggested that the development of the eggs under illumination was hastened by the heat radiated to them from the sources of illumination or conveyed to them by the air. Although such possible effects from radiation cannot be entirely dismissed considering the absorption spectrum of water, it seems quite likely that effective radiation would have been limited to bands within the visible spectrum. Certainly the more rapid hatching was not caused by a higher temperature of the water; there were no differences to the nearest hundreth of a degree. In view of the results of Embody (1934), Hayes (1949), and Price (1940) on the temperature-dependent rates of development of salmonid and coregonid eggs, the difference of 7–8 days in dates of hatching would have re-

quired a difference in temperature of about 0.5°C in the range of 2–4°C acting over a period of 3–5 months.

The difference of a few hours in the times of hatching of samples removed periodically from the dark and illuminated jars and incubated at room temperatures suggests that the illumination had hastened the developmental rates somewhat, but the greater difference of 7–8 days in the final results suggests that illumination was effective principally in stimulating the activity of the embryos, which by this time were ready to hatch, and the activity caused a mechanical rupturing of the egg capsules. In the absence of further information, it is not possible to state which organs or systems of the embryo responded to the illumination.

In comparison to the extremes of continuous illumination and essentially continuous darkness employed in the experiments, in nature the eggs experience smaller differences in illumination from one year to the next. The greatest differences generally would relate to the dates of formation and departure of the ice relative to the dates of spawning. Otherwise, the eggs can receive illumination only during the day. At no time while the lake is covered by ice, or ice and snow, would the eggs be likely to receive illumination at an intensity even approaching that of room illumination. Excepting the possibility that the date of hatching might be influenced by illumination if the ice departed from the lake at an unusually late date, the differences of 7–8 days obtained in the laboratory seem to have no application in estimating the dates of hatching in the lake. During the course of these studies, eggs in the lake never hatched under the ice.

The general patterns of incubation temperatures encountered in Lake Mendota are shown in Figure 1. As mentioned earlier, the actual temperatures in the lake at the depths occupied by the eggs generally are at least 1°C lower than in the laboratory. As a rule, the eggs are exposed to a period of higher temperatures during the early stages and again during the later stages of incubation. But the patterns of temperatures during these two terminal intervals vary appreciably from year to year. The date of hatching is not significantly altered by differences in temperatures encountered during the early stages from one year to the next. In comparing the most extreme patterns observed in this study (Fig. 1) the temperatures stood substantially apart for only about two weeks subsequent to December 12, the date of fertilization of the eggs in 1953, and this led to a difference of about 26 degree-days, roughly the equivalent of 1°C acting through a period of 25 days. The eggs in 1950–51 presumably would have hatched two days later than those in 1953–54, all other things being equal. Since the peak of spawning activities had occurred about a week earlier in 1950 than in 1953, it would be well to consider the algebraic sum of differences in temperatures between December 2, the date of fertilization in 1950, and December 30, the date on which the lake froze over in 1953. This amounts to about 14 degree-days, which is about equivalent to a difference of 0.5°C acting over a period of 25 days, and would expectedly have advanced the hatching date by one day for the eggs in 1953–54.

In view of the highly variable patterns of temperatures subsequent to the early stages of incubation, the difference of 1 or 2 days induced by thermal differences seems to have no application in estimating the date of hatching. The fact is, during the middle period of lower temperatures advanced embryos appear to lie dormant or continue to develop at a rate suggesting dormancy, while the retarded embryos proceed in their development at a higher rate. The results obtained with the eggs of *Coregonus clupeaformis* (Price 1940) indicate that from the time the eyes become pigmented the embryos continue to develop at proportionate rates throughout a range of constant temperatures. Therefore the differences in the time of appearance of these pigments would be maintained and expressed in the times of hatching. The fact that this did not hold true with the cisco, a point that was strongly illustrated in the experiment where eggs had been developed

to about the hatching stage by January 5 but remained unhatched at low temperatures until April, suggests the application of the term dormancy.

It is clear from a consideration of the data obtained demonstrating that the temperatures in the lake were lower than in the laboratory, that the eggs never hatch under the ice in this present climatic era. It is difficult to estimate when they should hatch because they are subjected to the combined effects of factors that individually shorten the incubation period. Following the departure of the ice they are exposed to relatively high illumination, to mechanical agitation by wave action, and generally to rising temperatures.

Excluding the effects of illumination and mechanical agitation and considering only those of temperature, it is substantially clear that the eggs never hatch prior to April 15 regardless of the date on which the ice leaves the lake. They probably do not hatch until about the first week in May. The eggs of *C. clupeaformis*, in the range of 0–6°C, hatch about 25–30 days apart when incubated for the duration of the period at constant temperatures differing by 1°C (Price 1940). Applying these results to the cisco, subsequent to the date of hatching in the laboratory the eggs in the lake should require at least an additional 50 degree-days to hatch. At temperatures in the range of 4–5°C this sum would accrue in 10–12 days. Hatching would occur no earlier than April 25.

According to Pritchard (1931) the cisco of Lake Ontario hatch between late April and early May. Insofar as they spawn sometime during the last 2 weeks in November and the first 2 weeks in December, as do the cisco in Lake Mendota, it is quite probable that the findings on the cisco of Lake Ontario apply to the cisco of Lake Mendota.

Whether or not the eggs of the cisco have ever hatched under the ice in Lake Mendota is a difficult question to answer. Records on file with the U. S. Weather Station at Madison show that since 1880 the latest date of thaw has been April 21, the earliest freeze December 3, and the maximum duration of ice-cover 124 days. Prior to 1880 the maxima for ice-cover were 151 and 162 days. In this study of a mean temperature of 2.4°C the eggs of the cisco hatched in 125 days. During this same time the mean temperature in the lake at the depths occupied by the eggs probably was around 1.6°C. The eggs of *C. clupeaformis*, incubated at 2°C required 133 days to hatch (Price 1940). They probably hatched prematurely, as Price noted, because they were kept in constant agitation in the incubation jars. Embody (1934) incubated lake trout eggs at 1.5°C for 166 days. At the same temperature the eggs of brown trout required 160 days, and the eggs of brook trout 146 days. If these findings on trout represent what might be found with cisco, possibly on the occasional year prior to 1880 the cisco did hatch under the ice in Lake Mendota, but in view of the delayed hatching produced by refrigeration of advanced eggs, the question cannot be answered without additional information.

The results of the experiments on the feeding habits of larval cisco do not suggest that year-class failures in Lake Mendota originate through starvation either as a consequence of the eggs hatching under a cover of ice or because of an inadequate food supply for the larval fish. It is quite evident that the eggs have not hatched under the ice since 1900 at least. However, if the eggs should hatch under the ice, the fact that the larval fish fail to obtain living zooplankton in darkness cannot be extended to describe the outcome under the ice because the minimum requirement of illumination was not determined. It is probable that the larval cisco require relatively bright illumination, for Einsele (1941) states that larval whitefish starved when supplied with an abundance of living zooplankton at a level of illumination that enabled him to read the printed matter in a book.

However, under no circumstances in Lake Mendota, is it likely that the larval fish encounter serious shortages of food. Their ability to tolerate starvation for 18 to 20 days at temperatures encountered after the ice has disappeared and for some 30 days at temperatures under the ice signifies that

they require no food until about the second week in May, by which time the crop of planktonic crustacea has about reached a maximum level (Birge 1897).

During the first week or two after hatching they should face no problems in obtaining food, for not only does the lake contain a rich variety of particulate matter, including phytoplankton, but also the large crop of zooplankton probably creates an abundance of dead or dying zooplankters. In view of this possibility it would seem unwise to estimate the conditions for survival of larval whitefishes in any lake solely on the basis of the standing crop of zooplankton.

Although the larval cisco obtain their fill on dead organisms more readily than on living organisms, the advantage is of questionable significance because in 5 or 6 days after hatching, while they still possess some material in the yolk sac, they capture living organisms about as rapidly as they do the dead ones.

Many edaphic factors on the watershed of Lake Mendota have been changed through the influence of man. Two villages empty treated sewage into the lake and the prairie was plowed permitting erosion to carry in many tons of fine sediments. We did not attempt to measure such influences on the early life history of cisco. That they might play a role must be acknowledged, but another study will be necessary to appraise such effects.

SUMMARY

1. It has been postulated that the decline of the cisco in Lake Mendota was caused basically by poor recruitment of young fish to the mature population. It has been assumed in these studies that poor year-classes have not been caused by the failure of the adults to spawn successfully.

2. The hypothesis that poor year-classes might arise through starvation of the larval fish when the eggs hatch under the ice during unusually late springs has been disproved.

3. The eggs do not hatch under the ice and it is doubtful that they ever have in the past 70 years. Taking into account variations in the annual patterns of incubation temperatures, it is estimated that the date of the hatch falls no earlier than April 25.

4. The dates of hatching are apparently unrelated to the dates of spawning, the dates of formation and departure of the ice, or the temperatures of the water prior to the freeze-over. Eggs incubated for 25 days from the time of fertilization at temperatures differing by 1°C in the range of 1–6°C, and then incubated at a common lower temperature hatched about 2 days apart.

5. Eggs that appeared to be ready to hatch were held for about 3 months at temperatures varying between 1.5 and 3°C without hatching. The embryos had remained dormant.

6. The dates of hatching may be substantially altered by annual differences in temperatures during the late stages of the incubation period. Eggs incubated for the last month of the period at temperatures differing by 1°C in the range of 2–6°C hatched about 7 days apart.

7. Eggs subjected to continuous illumination, in contrast to those held in continuous darkness, hatched 7 to 8 days earlier. Apparently the illumination did not accelerate the developmental rates to this extent, but rather stimulated the activity of the embryos that were ready to hatch.

8. Larval cisco apparently require illumination in order to feed on living zooplankton provided the concentrations of the food organism are not unreasonably high. If the larvae are kept in continuous darkness they starve. This confirms Einsele's observations on the European *Coregonus*.

9. At temperatures between 14 and 18°C, the larvae begin to swallow water and to feed on particulate matter during the day of hatching. By the third day they begin to consume adult *Cyclops* sp. During the first week they are more successful in feeding on dead zooplankton kept in suspension than on living zooplankton, but by the end of the week, they appear to feed equally well on living zooplankton. Their success in obtaining living zooplankton depends on the comparative swimming ability of the prey.

10. The larvae begin to feed before the yolk sac has been absorbed. At temperatures varying between 14 and 18°C, the yolk sac is absorbed in about 6 days.

11. At temperatures encountered after the departure of the ice, the larvae tolerate 18–20 days (108–128 degree days) of starvation. At temperatures between 3 and 4°C they withstand 30 some days of starvation.

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Estimates of the Minimum Size-Limit for Maximum Yield and Production of Chain Pickerel, *Esox niger* LeSueur, in Rhode Island[1]

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ABSTRACT

Mortality rates for chain pickerel were deduced from weighted geometric means of age frequencies in an unexploited and an exploited population. Fishing mortality was considered to be the difference between the two total mortality rates. Calculated growth in length and weight was determined for a composite sample from 32 ponds. Relative yields were computed for six different size-limits and two rates of fishing. It was found that a minimum size-limit of approximately 12 inches (total length) was best. A ratio of production to relative yield was determined, which indicated that less than 39 per cent of total production was removed as crop. Management suggestions were made on the basis of these data.

INTRODUCTION

Aquatic biologists are becoming increasingly interested in various aspects of the production as well as mortality rates of animals in inland waters. Often investigations are directed at the regulation of a particular species of fish in a rational manner. The investigation described herein has this as a primary objective.

Although highly informative accounts concerning the biology of chain pickerel have been given by Raney (1942), Foote and Blake (1945), Underhill (1949), and the New Jersey Fisheries Survey (1950), only Smith and Gross (1955) have attempted to evaluate the effects of various size-limits on yield as well as on standing crops of this fish. In the present study data obtained during a survey of Rhode Island's inland waters were considered satisfactory for deducing a minimum size-limit for optimum yield as well as an estimate of total production of chain pickerel as related to yield under the observed conditions. Inasmuch as this species is still being actively managed and investigated with varying degrees of objectivity, computation of the above-mentioned parameters from estimates of natural-mortality rate, rate-of-fishing mortality, and growth rate seems especially relevant at this time. The notation used in this paper follows that of Ricker (1948) as much as possible.

[1] Federal Aid to Fish Restoration funds were used for this problem under Dingell-Johnson Project F-2-R-3.

MORTALITY COMPONENTS

Total-mortality rate was first estimated as the weighted geometric mean of a sample of age frequencies as outlined by Rounsefell and Everhart (1953). A sample of an unexploited population of chain pickerel was obtained from Larkin Pond, a 44-acre pond in South Kingston, Rhode Island. This body of water is generally similar to several others in the state containing chain pickerel in respect to the physical and chemical variables which have been measured. The chain pickerel were obtained by means of a large fyke net which was fished for 20 days. Part 1 of Table 1 illustrates a comparison of unweighted and weighted geometric means of instantaneous total-mortality, survival, and annual-mortality rates for this pond. The weighted values are believed to be the better averages of ratios under the conditions at hand, and they have been utilized throughout. Both in Table 1 and in the text weighted values are indicated by (w). The total-mortality rate and natural-mortality rate in this lake

TABLE 1. *Computation of mortality and survival rates from Larkin Pond (Part 1) and Wallum Lake (Part 2) chain pickerel data*

Comparison of unweighted and weighted geometric mean values. The mathematical symbols used are those employed by Rounsefell and Everhart (1953). In Column H, D is weighted by square root of smaller f-value in each pair of comparisons.

A Age	B Age frequency	C Log of age frequency	D Log of $f(y)$ minus log $f(y-1)$	E D times 2.303 (sign changed)	F 1 + D	G Antilog of F	H D weighted
y	f	log f	log $1/s$	i	(log s) + 1	$s(y)$	log $(1/s)(w)$
			Part 1—Larkin Pond				
IV	18	1.2553					
V	12	1.0792	−0.1761	0.4056	0.8239	0.6667	−0.6110
VI	7	0.8451	−0.2341	0.5391	0.7659	0.5874	−0.6192
VII	3	0.4771	−0.3680	0.8475	0.6320	0.4285	−0.6364
VIII	1	0.0000	−0.4771	1.0988	0.5229	0.3334	−0.4771
					unweighted	weighted	
	instantaneous mortality		(i)		0.72	0.61	
	survival		(s)		0.50	0.54	
	annual mortality		(a)		0.50	0.46	
			−1.2553		2.7447		−2.3437
		−1.2553/4 =	−0.3138	0.7228	0.6862	0.5030	
					−2.344/8.84 =	0.265	
			Part 2—Wallum Lake				
II	32	1.5052					
III	12	1.0792	−0.4260	0.9840	0.5740	0.3750	−1.4755
IV	4	0.6021	−0.4771	1.0988	0.5229	0.3334	−0.9542
V	2	0.3010	−0.3011	0.6934	0.6989	0.5000	−0.4257
VI	2	0.3010	0.0000	0.0000	0.0000	0.0000	0.0000
					unweighted	weighted	
	instantaneous mortality		(i)		0.69	0.79	
	survival		(s)		0.30	0.45	
	annual mortality		(a)		0.70	0.55	
			−1.2042		1.7958		−2.8554
		−1.2042/4 =	−0.3013	0.6944	0.4489	0.3021	
					−2.855/8.29 =	−0.34	

are synonymous, because no fishing had been permitted in the pond for several years.

The same method was used for computing weighted and unweighted mortality components and survival from an exploited fish population and is illustrated in Part 2 of Table 1. This sample was obtained from chain pickerel killed during the chemical reclamation of a 320-acre pond located partly in Rhode Island and partly in Massachusetts. Computation of the instantaneous and annual mortality rates from fishing is done by simply subtracting the two instantaneous total mortality rates in the following manner:

$i\,(w)$ exploited population = 0.79
$i\,(w)$ unexploited population = 0.61
p = instantaneous fishing mortality rate = 0.18
m = annual fishing mortality rate = $1 - e^{-p}$ = 0.16
q = instantaneous natural mortality rate = $i\,(w)$ unexploited = 0.61

It is recognized that these estimates of mortality may be subject to distortion due to inaccuracies in reading scales, sample size, gear selectivity, and variations in strength of year-classes. It is further

assumed that the observed natural-mortality rate and fishing-mortality rate are somewhat representative of conditions in the State. For reasons which follow it is believed that none of these factors completely invalidates estimates of the components of total mortality that have been made. That the age of chain pickerel cannot be estimated with complete accuracy is appreciated. However, independent determinations of ages from scale reading reveal only a fraction of the difference between true age and that derived from scale reading because the real difference is usually underestimated. It was found that the uncertainty of age determinations increased with older fish. The effects of various errors in age determinations have been computed from mathematical models by Gulland (1955). The error which was encountered in this instance, of increasing uncertainty of age determination with increasing age of the fish, tends to overestimate survival rate, but usually not to the extent where it appears useless to compute in practice. Although the sizes of both samples are not numerically great, they represent 15 and 28 per cent, respectively, of the total estimated population (10 inches *TL* or greater) from these ponds. In order to avoid sampling error, eight fish (Age III-7, Age II-1) were eliminated from the Larkin Pond sample. Twenty-four Age I chain pickerel were eliminated from the Wallum Lake data. Finally, in the computation of relative yield, the observed fishing-mortality rate was experimentally manipulated over a fairly large range of values without materially affecting the conclusions concerning minimum size limits for optimum yield. It was necessary to assume that dominant year-classes were not present in these samples.

GROWTH

Growth was estimated from a sample of 257 chain pickerel from 32 Rhode Island ponds. No more than 20 specimens from a single body of water were used. The method of capture was primarily by fyke nets. Growth was calculated from scale measurements in order to avoid effects of selective sampling which could have been brought about by net selection for larger individuals in the younger age-classes. Furthermore, observed growth would have been unsatisfactory because the sampling period extended over the entire season. Differential growth according to sex has been observed in the chain pickerel by several investigators. For the purposes at

TABLE 2. *Regression of scale length* (X) *on fork length* (Y) *for 257 chain pickerel from 32 Rhode Island ponds*

Frequency X		4	8	18	32	30	36	48	25	26	17	7	5	1	N = 257
15	460–79								1	1	1				3
14	440–59							3	4	7	2	1	1		18
13	420–39							1	3	3	6	3	2		18
12	400–19						2	3	2	5	4	1			17
11	380–99					2	3	7	2	2	1	1	1		19
10	360–79					5	5	8	3	2		1	1		25
9	340–59				3	4	4	12	4	1	3			1	32
8	320–39				2	5	5	8	3	3					26
7	300–19			2	6	9	10	4	1	2					34
6	280–99			4	8	2	4	2	2						22
5	260–79			2	8	1	3								14
4	240–59		1	7	4	2									14
3	220–39		3	3	1										7
2	200–19	1	3												4
1	180–99	3	1												4
	Actual Classes	60–9	70–9	80–9	90–9	100–9	110–9	120–9	130–9	140–9	150–9	160–9	170–9	180–9	Frequency Y
Coded Classes		1	2	3	4	5	6	7	8	9	10	11	12	13	

TABLE 3. *Tests of significance for linear regression and deviation from linearity for chain pickerel body-scale relationship*

	Sum of squares	Degrees of freedom	Mean square	Variance ratio
1. Analysis of variance for significance of regression				
Regression	1701.33	1	1701.33	434*
Error	1002.67	255	3.93	
Total	2704.00	256		
2. Analysis of variance for deviation from linear regression				
Regression	1701.33	1	1701.33	
Deviation from Regression	74.24	11	6.75	1.77
Error	928.43	243	3.82	

hand, estimates of average length and weight of a year-class were made without accounting for sex differences.

The first consideration in calculated growth involves the determination of a body-scale relationship. The individual measurements were divided into suitable class intervals and a regression table (Table 2) of fork length (Y) on the magnified scale image (X) was made according to a method outlined by Goulden (1952). Tests of significance for linear regression as well as deviation from linearity were made for the observed body-scale relationship. The results of these are shown in Table 3. In the analysis of variance for significance of the regression the observed mean square for linear regression clearly indicates that a regression line could be fitted to these data. Next, a test for deviation from linearity was made. It is noted that the deviation from linearity is nonsignificant, which indicates that a straight line rather than some other function can be fitted to these data. The above method is suggested for determining a body-scale relationship since it avoids visual inspection to determine the fit of a line to experimental data as well as the more laborious computation of a polynomial expression unless it is necessary. The regression equation for coded class values was found to be:

$$Y = 1.886 + 1.043\ X$$

Back calculations of length to observed annuli were made according to Lee's method which is described by Lagler (1952) using a correction factor of 37.7 mm (a positive Y intercept of 37.7 mm). A plastic overlay nomograph as described by Lowry (1951) was constructed and used for back-calculations.

A source of error (Lee's phenomenon) may occur in calculated growth studies. In a visual comparison of back-calculated lengths to Age I from Age V, VI, VII, and VIII chain pickerel versus back-calculated lengths to Age I from Age II fish, it was observed that the calculated lengths to Age I from the older fish appeared to be smaller than from the younger fish. A formal test of the extent of differences between these two groups was made by means of the t-test. The observed t-value of 2.83 (58 d.f.) in this comparison of two sets of measurements indicated the presence of Lee's phenomenon by the low probability (0.01) of a larger value of t. A similar comparison of back-calculated lengths to Age I from Age IV fish versus the back-calculated lengths to Age I from Age II fish gave a t-value of 2.37 (60 d.f.) indicating a probability of somewhat less than 0.05 for a larger value. In plotting the calculated growth curve, back-calculated lengths to Age I, II and III were derived from Age IV and younger chain pickerel, whereas back-calculations to Age IV were made from older fish. The calculated growth of chain pickerel from Rhode Island is shown in Figure 1. Since computations of production and relative yield are made in terms of weight, it is necessary to transform these data into growth in weight. A length-weight relationship for these chain pickerel was calculated by the least squares method according to Snedecor (1946) after transforming lengths and weights to common logarithms of these values. The relationship obtained is described by the formula:

$$\text{Log } W = -5.5101 + 3.1304 \text{ Log } FL$$

where W is the weight in grams and FL is the fork length in millimeters. Growth in length was converted to growth in weight by means of this equation. The logarithms of weights were then plotted against age. The resultant curve (Fig. 2) is an indication of the instantaneous rate of growth of this

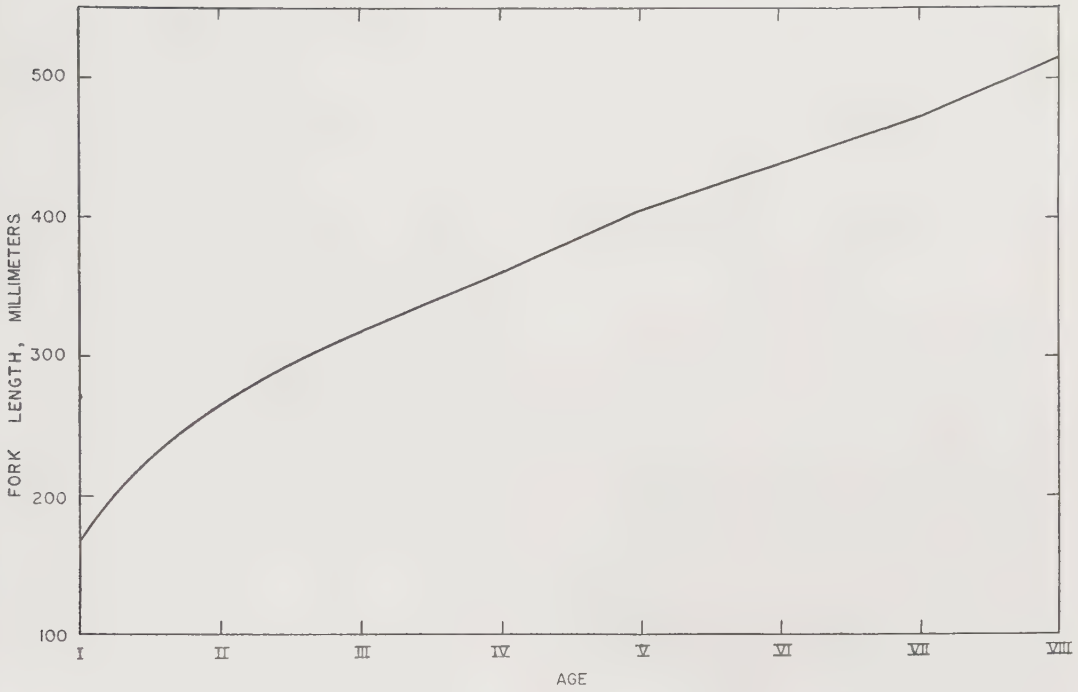

FIG. 1. The calculated growth curve for 257 chain pickerel from 32 Rhode Island ponds.

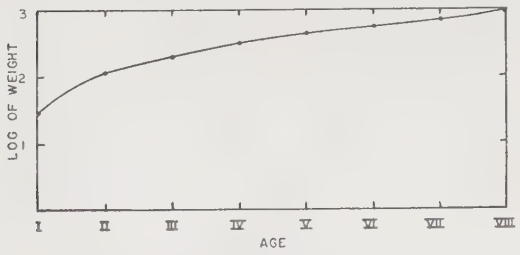

FIG. 2. The instantaneous growth of 257 chain pickerel from 32 Rhode Island ponds.

population. In order to make the observed mortality rates and growth rate strictly comparable, values of the slope of this curve were transformed to the base e by simple multiplication by 2.303 ($\log_e 10 = 2.303$) giving values of k, the instantaneous rate of growth, in exponential form.

RELATIVE YIELD

Several methods of computing a size-limit for a fishery in order to permit a maximum sustained yield have been formulated on various assumptions regarding growth and mortality by Ricker (1945), Allen (1953), and Beverton (1953). In this instance the assumption of exponential growth and mortality has been made, and Ricker's method has been used for computing minimum size limits for maximum yield.

Growth and mortality rates were divided into quarter-year increments and computations of relative yield were made according to the example given in Table 4 which illustrates the effects of a fifteen-inch size-limit and the observed fishing rate on relative yield. These computations were made for two rates of fishing and for six different size limits. The results of these are as follows:

Minimum Size total length, inches	Rate of fishing (p)	
	0.4	0.2
10	243	158
11	246	171
12	252	169
13	230	150
14	212	132
15	141	81

It is apparent from these data that a minimum size of approximately 11 inches total length permits the highest relative yield at

TABLE 4. *Instantaneous rates of growth* (k), *natural mortality* (q) *and fishing mortality* (p), *at quarter-year intervals for chain pickerel in Rhode Island, and the computation of relative yield*

1 Age	2 $\bar{x}$ *FL* (mm)	3 $\bar{x}$ wt (g)	4 k	5 q	6 $k-q$	7 p	8 $g=(p+q)$	9 $g/4$	10 $e^{g/4}-1$	11 weight change	12 Pop. wt.	13 Av. wt.	14 Catch (Y)
											100		
I	167	28	2.3	0.6	1.7	0	1.7	0.425	0.529	53	153	126	0
I¼	200	49	1.6	0.6	1.0	0	1.0	0.250	0.284	43	196	174	0
I½	230	81	1.4	0.6	0.8	0	0.8	0.200	0.221	43	239	218	0
I¾	250	104	1.2	0.6	0.6	0	0.6	0.150	0.162	39	278	258	0
II	267	120	0.9	0.6	0.3	0	0.3	0.075	0.078	22	300	289	0
II¼	278	136	0.7	0.6	0.1	0	0.1	0.025	0.025	8	308	304	0
II½	292	162	0.7	0.6	0.1	0	0.1	0.025	0.025	8	316	312	0
II¾	305	180	0.7	0.6	0.1	0	0.1	0.025	0.025	8	324	320	0
III	316	200	0.5	0.6	−0.1	0	−0.1	−0.025	−0.023	−7	317	320	0
III¼	327	220	0.5	0.6	−0.1	0	−0.1	−0.025	−0.023	−7	310	313	0
III½	338	236	0.4	0.6	−0.2	0	−0.2	−0.050	−0.048	−15	295	302	0
III¾	348	260	0.4	0.6	−0.2	0	−0.2	−0.050	−0.048	−14	281	288	0
IV	358	284	0.4	0.6	−0.2	0	−0.2	−0.050	−0.048	−13	268	274	0
IV¼	370	312	0.4	0.6	−0.2	0	−0.2	−0.050	−0.048	−13	255	262	0
IV½	382	354	0.4	0.6	−0.2	0.2	−0.4	−0.100	−0.094	−24	231	243	12
IV¾	392	388	0.4	0.6	−0.2	0.2	−0.4	−0.100	−0.094	−22	209	220	11
V	405	430	0.4	0.6	−0.2	0.2	−0.4	−0.100	−0.094	−20	189	199	10
V¼	412	460	0.4	0.6	−0.2	0.2	−0.4	−0.100	−0.094	−18	171	180	9
V½	419	488	0.2	0.6	−0.4	0.2	−0.6	−0.150	−0.139	−24	147	159	8
V¾	425	500	0.2	0.6	−0.4	0.2	−0.6	−0.150	−0.139	−20	127	137	7
VI	436	554	0.2	0.6	−0.4	0.2	−0.6	−0.150	−0.139	−18	109	118	6
VI¼	442	572	0.2	0.6	−0.4	0.2	−0.6	−0.150	−0.139	−15	94	102	5
VI½	452	620	0.2	0.6	−0.4	0.2	−0.6	−0.150	−0.139	−13	81	88	4
VI¾	467	680	0.2	0.6	−0.4	0.2	−0.6	−0.150	−0.139	−11	70	76	4
VII	472	715	0.2	0.6	−0.4	0.2	−0.6	−0.150	−0.139	−10	60	65	3
VII¼	482	774	0.4	0.6	−0.2	0.2	−0.4	−0.100	−0.094	−6	54	57	3
VII½	492	826	0.4	0.6	−0.2	0.2	−0.4	−0.100	−0.094	−5	49	52	3
VII¾	504	890	0.4	0.6	−0.2	0.2	−0.4	−0.100	−0.094	−5	44	46	2
VIII	515	953	0.4	0.6	−0.2	0.2	−0.4	−0.100	−0.094	−4	40	42	2
												Total:	81

the observed rate of fishing whereas an increase in the rate of fishing to 0.4 ($m = 1 - e^{-p} = 0.33$) permits a maximum yield at 12 inches. These figures represent annual fishing mortalities from 16 to 33 per cent. Although higher fishing mortalities may occur these are believed to be exceptions to the general case. The relatively small difference between relative yields for minimum size limits between 11 and 12 inches at a fishing rate of 0.2 is to be noted. Evidence at hand indicates that the existing size limit of 12 inches in Rhode Island is probably the best one under present conditions.

PRODUCTION

Using the expression developed by Ricker (1945)

$$B = \frac{kP_0(e^{k-i} - 1)}{k - i}$$

where B is the total production for a year and P_0 is the weight of the stock of fish at time $t = 0$, the yield is equal to

$$Y = P_0 e^{k-i}$$

where Y is the yield when the yield of fish at the end of a year is equal to the standing crop at the end of this period. The ratio of production to yield then equals

$$\frac{B}{Y} = \frac{\dfrac{kP_0(e^{k-i} - 1)}{k - i}}{P_0 e^{k-i}} = \frac{k}{k - i}(1 - e^{-(k-i)})$$

The direct estimation of the production of chain pickerel in Rhode Island is not

possible using population estimates because in this instance the population was obtained from several (32) bodies of water and estimates of the standing crop of pickerel were attempted in only two instances. However, an approximate relationship between the relative yield obtained under the observed conditions and production as related to relative yield can be postulated using the B/Y ratio above. Using this expression the relative value for production has been computed for quarter-year intervals for chain pickerel of approximately 12 inches and greater for the balance of their known life history. The total production of these fish equalled 140 weight units versus 169 weight units of yield since exploitation began at the observed rate of fishing. It is interesting to note that the yield is greater than production during this time, but a standing crop of 289 weight units exists at the time the fish become vulnerable to fishing. Of course, the total production necessary to produce a standing crop of this magnitude is considerably greater than 289 weight units. Therefore, the relative yield under these conditions must have been considerably less than:

$$\frac{169}{140 + 289} \times 100 \text{ or } 39 \text{ per cent}$$

of the total production.

These figures present some insight into the problems of fisheries management pertaining to the chain pickerel. For example, from the relationship between production and yield, the addition of artificially propagated chain pickerel into ponds and lakes cannot increase the average size of individuals or yield on a sustained basis, because the rate of removal exceeds production during this stage of pickerel life history even under moderate fishing intensity. Thus, there seems to be little justification for artificial propagation of chain pickerel, even to approximately legal size if this procedure is intended to produce lasting effects. Furthermore, the available information on the relation of production to yield suggests that there probably has been a significant reduction in the average size of individuals due to increased fishing intensity since the "good old days" when large fish were said to be far more common than now. If a larger fish is considered highly desirable, then a reduction of fishing effort (a smaller bag-limit) is suggested as a management possibility. Although no data are available as yet to indicate the relationship between the number of spawning adult chain pickerel and recruitment, a reduced bag limit would probably increase the size of the brood stock to some extent also.

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Vitamin B_{12} in Suspended Solids and Marsh Muds Collected Along the Coast of Georgia[1]

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ABSTRACT

Vitamin B_{12} content of suspended solids in river and sea waters and in marsh muds, collected along the coast of Georgia, was determined by means of the *E. coli* mutant assay. Appreciable amounts of vitamin B_{12} are carried on suspended particles of river water, the brown water types showing highest concentrations, up to 6.4 μg per gram of solids. Vitamin B_{12} content of particulate matter in the sea waters varied over the range 0.0027 to 0.130 μg per liter. Calculated in relation to dried solids, the highest concentration of B_{12} was 0.736 μg per gram of solids. Considerable variations were found at different times, stations, and depths. Samples of suspended matter taken from the Duplin River at different phases of the tide showed maximal values of B_{12} up to about 0.06 μg per liter, on the outgoing tide. In settling experiments it appeared that a major portion of B_{12} is correlated with the organic fraction of solids in sea water. Enrichment cultures showed large increases of vitamin B_{12} produced by microorganisms in marine muds and waters. Many isolated bacteria were grown on extracts of marsh grass and found to produce significant quantities of the vitamin. It is concluded that suspended particles are important in the vitamin nutrition of the sea and that bacteria are significant producers and carriers of vitamin B_{12} in the marine environment.

The coastal waters of Georgia are important for studies of biological productivity because of the numerous shallow estuaries and large areas of marsh grass in this region. Great rivers, such as the Savannah and the Altamaha, carry from the eroded land large amounts of suspended particles and dissolved materials down into the sea, where the estuarine waters generally show considerable turbidity. Saltmarsh grass, *Spartina*, growing extensively over the marsh lands contributes on a large scale to primary productivity in the region. The phytoplankton also attains heavy growth in certain seasons when the transparancy of the water and other conditions are favorable. Conversion of this primary plant matter into products available for marine communities of animals appears to be mediated mainly by heterotrophic microorganisms, especially marine bacteria. Availability of numerous microbial products to plant and animal life in the coastal waters, and the further contribution of food and dissolved nutrients from the shallow waters to the oceanic environment constitute problems which we have undertaken to study. Any consideration of the role of microorganisms and growth factors in the nutritional cycle of the sea would naturally include the biological relations of catalytic substances, such as the B vitamins. Among these compounds vitamin B_{12} constitutes one of the most potent of known growth stimulating substances. Cyanocobalamine, the chief natural vitamin B_{12}, appears to be synthesized mainly by bacteria and fungi, and is required for growth by many microorganisms, animals, and man (Sebrell and Harris 1954). The importance of vitamin B_{12} in biological productivity of the sea is suggested by the occurrence of this vitamin in marine invertebrates (Maxwell 1952, Robbins *et al.* 1951) and in fish (Tarr *et al.* 1950), and its requirement for growth by numerous bacteria (Stoksdad *et al.* 1955), algae and protozoa (Hutner and Provasoli 1951, Sweeney 1954, Lewin 1954, Wilson and Collier 1955). It appears highly probable that red tide flagellates are stimulated to form blooms by outwash of vitamin B_{12}

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from the land. The pelagic diatom, *Skeletonema costatum*, requires cobalamine for growth (Droop 1955). A review of the chemistry and biological relationships of vitamin B_{12} by Ford and Hutner (1955) and a discussion of the nutritional requirements of algal flagellates by Provasoli and Pintner (1953) indicate the great physiological and ecological significance of the vitamin B_{12} group of substances.

The purpose of this paper is to report on the occurrence of vitamin B_{12} in marsh muds and suspended particles in river and sea waters in the coastal region of Georgia. It is hoped that the data presented here may be of value to those concerned with the succession of plankton communities and general productivity in the sea.

MATERIALS AND METHODS

Samples of mud and water were collected during the summer and autumn of 1955 from different stations located along the coast between Savannah, Georgia and Jacksonville, Florida. The muds were scraped from the surface of marsh land, and the water samples were collected by dipping from the surface or by pumping from lower depths with a centrifugal pump and hose. Samples of mud were dried at 35° C in front of a heating fan. Particulate matter in the water samples was separated on millipore filters and dried rapidly in an oven at 100° C for determination of dry weight. Duplicate samples of filtered particles dried at 35° C were used for determination of vitamin B_{12}, employing the *Escherichia coli* mutant 313. This assay organism was selected because of its response to the principal forms of vitamin B_{12} (Stoksdad *et al.* 1955). Assays were performed on sulfite-treated samples, because of the consistent, increased yields obtained. Details of the methods are to be found in another communication (Burkholder and Burkholder 1956). All dried samples were stored in a desiccator over dry $CaCl_2$ until assays could be made.

Loss on ignition was determined by ashing the filters and their adhering detritus in a muffle furnace at 750°. Corrections for the presence of salt in the wet filters were made by subtracting "salt errors" from the apparent total dry weights and from the apparent ash weights. The difference between corrected dry weight and corrected ash weight gave the organic weight of the sample.

The values obtained in vitamin B_{12} assays of sulfite-treated samples of mud and suspended solids are reported herewith, along with some data on enriched cultures of microorganisms. Analysis of dissolved vitamin B_{12} present in these waters is under investigation and will be reported later.

SUSPENDED SOLIDS OF RIVER AND SEA WATERS

Table 1 shows the vitamin B_{12} content of the solids filtered from different samples of fresh water and sea water collected in October and November, 1955. Average salinity values are given for the samples taken at the different stations. Attention is called to the comparatively high dry weight of the suspended solids present in shallow waters of the outer beaches at Savannah, Sapelo, Sea Island, St. Simons Beach, Doboy Sound, and Sea Island, concurrent with the development of a pronounced bloom of diatoms in these waters. It is possible that at least some of the plankton diatoms (e.g. *Skeletonema* sp., according to Droop's recent work) were growing in response to an abundant supply of B_{12}. Vitamin B_{12} varied in these sea water samples from 0.105 to 0.736 μg per gram of dried solids. The average of 14 samples taken in October was 0.0093, and of 13 samples, taken in November, the average was 0.0300 μg per liter. Vitamin B_{12} in the suspended solids of all of these sea-water samples varied over the range of 0.0027 to 0.1300 μg per liter.

Considering the samples of brackish and fresh waters in the second part of Table 1, it is apparent that river waters, particularly those of the brown water type, carry suspended solids characterized by high concentrations of vitamin B_{12}. Suspended solids in the brown waters of such rivers as Canochee, Ogeechee, Satilla, Little Satilla, Nassau, St. Marys, and St. Johns (Jacksonville Harbor) ranged from 1.061 up to 6.400 μg of B_{12} per gm of dry weight in October. The values for total B_{12} in

TABLE 1. *Vitamin B_{12} in suspended solids of river and sea water, collected October and November, 1955, along the coast of Georgia*

SEA WATER	Salinity 0/00	October 22–26			November 25–28		
		Dry wt. mg/L	B_{12} μg/L	B_{12} μg/g	Dry wt. mg/L	B_{12} μg/L	B_{12} μg/g
Savannah Beach	28.8	207.4	0.0218	0.105	51.8	0.0168	0.324
Ft. Pulaski Bridge	18.4	19.2	0.0067	0.342	—	—	—
Lazaretta Creek	18.8	14.3	0.0096	0.670	25.7	0.0104	0.404
Waterway, Thunderbolt	17.9	10.9	0.0080	0.736	45.1	0.0200	0.488
Valona	—	—	—	—	63.5	0.0182	0.287
Sapelo Beach	29.2	33.2	0.0050	0.152	231.8	0.0500	0.216
Duplin River	28.1	12.6	0.0076	0.606	21.8	0.0080	0.368
Doboy Sound	24.8	8.3	0.0027	0.337	158.8	0.0400	0.252
Sea Island Beach	31.1	209.4	0.0225	0.107	512.4	0.0650	0.127
Cloisters, Sea Island	28.7	23.3	0.0050	0.215	12.2	0.0060	0.490
St.Simons Beach, King and Prince Hotel	29.5	154.9	0.0175	0.113	48.5	0.0104	0.214
Waterway, St. Simons	24.2	16.4	0.0035	0.214	21.6	0.0080	0.369
Brunswick River Old Bridge	19.1	8.9	0.0040	0.447	—	—	—
Brunswick River New Bridge	23.8	34.2	0.0093	0.273	—	—	—
Jekyll Island Beach	—	—	—	—	545.8	0.1300	0.238
Jacksonville Beach	32.7	49.4	0.0067	0.135	27.7	0.0080	0.289
Clark Hill Reservoir	0	2.3	0.0018	0.810	—	—	—
Savannah River, Route 28	0	3.6	0.0025	0.700	—	—	—
Savannah River, Route 301	0	12.5	0.0043	0.343	14.6	0.0036	0.246
Canochee River, Route 301	0	8.8	0.0128	1.460	—	—	—
Ogeechee River, Route 301	0	2.9	0.0022	1.460	—	—	—
Ogeechee River, Route 17	0	6.6	0.0070	1.061	13.7	0.0112	0.816
Sapelo River, Route 17	10.6	17.2	0.0105	0.612	17.6	0.0060	0.314
Darien River, Route 17	2.3	36.9	0.0150	0.406	40.8	0.0120	0.294
Altamaha River, Route 17	0.2	18.7	0.0105	0.563	41.6	0.0125	0.300
Altamaha River, Route 301	0	40.8	0.0132	0.323	—	—	—
Satilla River, Route 17	0	50.3	0.0419	0.764	273.7	0.0700	0.256
Satilla River, Route 1	0	13.9	0.0144	1.031	—	—	—
Little Satilla, Route 1	0	5.7	0.0072	1.268	—	—	—
Nassau River, Route 17	1.0	21.2	0.0145	0.764	24.4	0.0160	0.657
Nassau River, Route 1	0	1.3	0.0080	6.400	—	—	—
St. Marys River, Route 17	0.3	6.4	0.0175	2.716	1.2	0.0046	3.710
St. Marys River, Route 1	0	2.7	0.0075	2.712	—	—	—

suspended solids per liter were generally not higher in these river waters than in the sea waters reported in the first half of Table 1, but the concentration of B_{12} in the suspended particles of these brown waters appears to be very high. It should be pointed out that the dark-colored rivers were devoid of suspended clay at this time of year because of the low rainfall. Comparatively large amounts of suspended matter, as evidenced by the dry weights were present in the Darien, upper Altamaha, Brunswick, and Satilla rivers.

HORIZONTAL VARIATION OF VITAMIN B_{12}

Horizontal variation of vitamin B_{12} in the suspended matter collected in surface samples of water in the vicinity of Doboy Sound was studied on August 8, 1955. The sampling locations may be found on Chart 1241 of the U. S. Coast and Geodetic Survey. The resulting data, presented in Table 2, show a considerable variation of values, ranging from 0.0013 to 0.0107 μg per liter along a line of stations extending from buoy "ND" outside Doboy Sound to Meridian Dock in Hudson Creek at the head of the sound. Samples of surface water were studied from the Duplin River on August 26, 1955. The results (Table 2) show that, proceeding up the Duplin River from Doboy Sound, the vitamin B_{12} in the detritus and plankton, steadily increases from 0.006 at the mouth to 0.044 μg per

liter at the head of the river. Further considerations of the data suggest that variations in both the amount and kind of particulate matter influence the vitamin B_{12} values. Thus, variations in vitamin B_{12} in the samples of Doboy Sound seem to be related to the quality rather than the amount of suspended solids. In the Duplin River series, the B_{12} varies along with the quantity and quality of suspended matter. It seems probable that high levels of the vitamin in the upper reaches of a "dead" river, such as the Duplin River, may be correlated with microbial production and accumulation in the marsh areas. Ragotzkie and Pomeroy (unpublished) found that red tide blooms occur occasionally in this region.

VARIATIONS OF VITAMIN B_{12} IN A TIDAL CYCLE

In order to gain some idea about the fluctuation of vitamin B_{12} in suspended solids with change in the tide, samples of water were obtained from near the mouth of the Duplin River on August 22, 1955. Samples were taken from the surface, an intermediate level, and near the bottom at nine different times during the time interval 1141 to 2321, covering approximately one tidal cycle. Duplicate portions of each sample were filtered, one being used for B_{12} assay and the other for determination of dry weight. The essential vitamin B_{12} data are plotted, along with the tidal curve, in Figure 1. Two maxima may be seen in the vitamin values, plotted as μg per liter of water. One major peak occurred during the falling tide, and another minor peak was observed during the rising tide, presumably at times when the velocity of water movement resulted in greatest mixing of suspended matter in the water. When the concentration of vitamin B_{12} is plotted as μg per gram of dried solids, an increase is noted near low tide, when the water was comparatively still, and a certain amount of settling probably was taking place.

SETTLING OF SUSPENDED SOLIDS

An experiment was devised for the purpose of ascertaining the rate of settling of suspended solids and its effect upon vitamin B_{12} content. The plan of the experiment was to distribute uniform samples of water in 1 gallon containers, and then allow settling to take place over a period of six

TABLE 2. *Variations of vitamin B_{12} in suspended solids of surface samples of water collected in the vicinity of Doboy Sound, August 8, 1955, and from the Duplin River, August 26, 1955*

Location	Dry wt. mg/L	B_{12} μg/L
B "ND", Outside	16.1	0.0013
C "3B", Outside	—	0.0034
N6 Doboy Sound	15.2	0.0062
Old Tower, Doboy Sound	19.6	0.0066
Intracoastal Waterway, Doboy Sound	14.8	0.0072
Marsh Landing, Duplin River	19.6	0.0100
Meridian Dock, Hudson Creek	17.6	0.0107
Marsh Landing, Duplin River	13.4	0.0060
Sawmill, Duplin River	18.8	0.0088
West Fork Entrance, Duplin River	20.0	0.0128
¼ way up West Fork, Duplin River	26.0	0.0176
¾ way up West Fork, Duplin River	38.0	0.0320
Head of East Fork, Duplin River	51.0	0.0420
Head of West Fork, Duplin River	73.0	0.0440

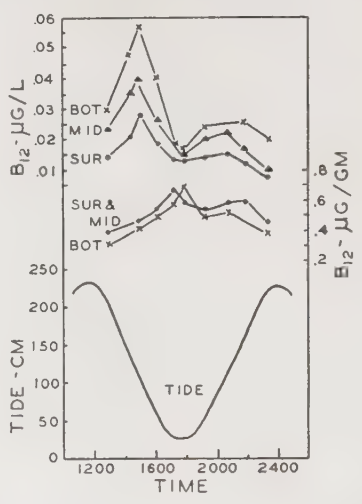

FIG. 1. Amounts of vitamin B_{12} found in suspended particles filtered from sea water at different levels of the tide, shown in cm above mean low water, August 22, 1955, mouth of the Duplin River, Sapelo Island, Georgia. Vitamin B_{12} is shown as μg/L of water taken from the surface (sur.), middle (mid.) and bottom (bot.), and as μg/gram of solids from the bottom, and an average for the surface and middle.

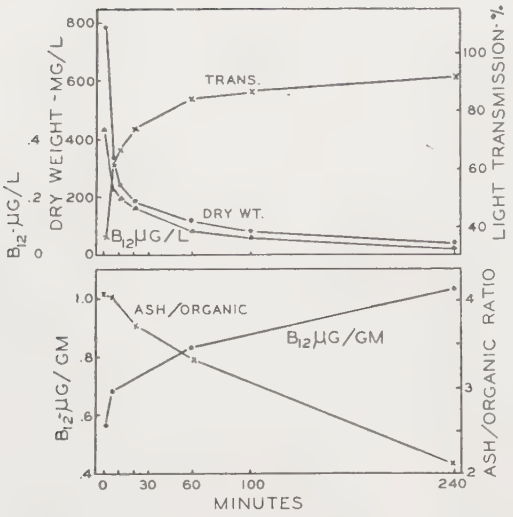

Fig. 2. Dry weight, transparency, ratio of ash/organic matter, and vitamin B_{12} in suspended particles filtered from the upper 3.5-cm layer of sea water allowed to settle in one gallon jugs for different periods of time (minutes). The water was obtained at low tide from the head of the West Fork of the Duplin River, August 29, 1955.

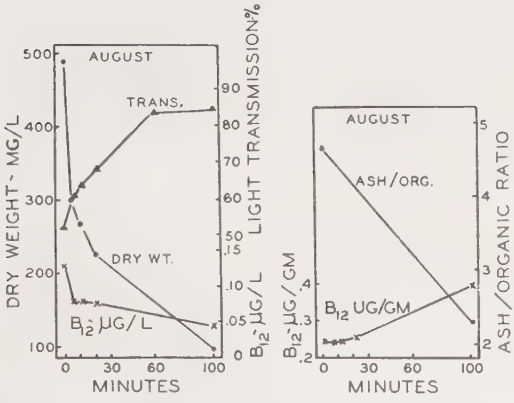

Fig. 3. Dry weight, transparency, ratio of ash/organic matter, and vitamin B_{12} in suspended particles filtered from the upper 3.5-cm layer of sea water allowed to settle in one gallon jugs for different periods of time. Water was obtained at ebb tide from a muddy margin of the Duplin River at Marsh Landing on August 28, 1955.

hours. At different time intervals the upper 3.5 cm layer of water was drawn off by a suction apparatus and kept for analyses. Only one sample of the upper layer was removed from each of the vessels, so that a time series of samples was obtained while the turbidity progressively decreased as a result of settling. The water samples were filtered through millipore filters for the purpose of collecting the solid particles, including detritus and plankton down to the size of bacteria. Transparency of aliquots was measured at 610 mµ in the Coleman spectrophotometer, using a tube 19 mm in diameter and distilled water as the standard. The dry weight, ash weight, organic matter, and vitamin B_{12} assays were made on duplicate samples. Settling experiments were done on surface water collected from near the mouth of the Duplin River on August 28, and again on November 28. A sample of surface water from the head of the West Fork of the Duplin River was also studied on August 29, 1955. Representative data, plotted in Figure 2, show clearly how the suspended matter decreases rapidly with time. The transparency of these waters actually increases, after settling for 12 hours, to the same value as distilled water. It can be concluded that the "muddy" appearance of the water is caused by the presence of brown suspended particles, and that when these settle out the supernatant becomes colorless and clear. This is not true of the brown water of certain rivers, discussed above, whose settled or filtered waters still retain yellow and brown pigment particles of very small size.

Further consideration of the data (Fig. 2) shows that vitamin B_{12} (µg per liter) decreases with disappearance of suspended matter. When the ratio of ash/organic matter is plotted against time of settling, the ratio decreases progressively, while concentration of the vitamin (µg per gm) increases. This suggests that vitamin B_{12} may be associated with the organic fraction of the suspended particles. The results obtained with samples of water collected at Marsh Landing near the mouth of the Duplin River, shown in Figures 3 and 4, are in general agreement with the other data on settling.

VITAMIN B_{12} IN MUD DEPOSITS

Marshlands along the coast of Georgia are classified by the staff of the Marine Biology Laboratory, Sapelo Island, into three main categories: high marsh, middle

marsh, and low marsh. The high marshland is relatively firm and is flooded for a short time only by high tides. It supports a yellowish green, short growth of *Spartina*. The low marsh occurs along the banks of rivers and is continuously flooded except at low tide. It consists of very soft mud, and supports lush, green growth of *Spartina*. Middle marsh lies somewhere between these two types in level, and in biological characteristics. In order to learn something about the production of growth factors in these muds, samples obtained from different locations were assayed for vitamin B_{12}. Results for three types of marsh mud collected on October 26, 1955, are shown in Table 3. Although some variation exists, the muds taken from these marsh areas appear to contain similar levels of vitamin B_{12}. Numerous assays on marine muds collected from many places along the Georgia coast indicate wide-spread presence of vitamin B_{12} in the dark muds and lesser values in the light, sandy areas. Other samples were collected August 26, 1955, from two kinds of low marsh areas where algae were growing either abundantly or sparsely for the purpose of learning whether vitamin B_{12} levels might be correlated with the presence of autotrophic thallophytes. The data, presented in Table 4, support the view that vitamin B_{12} is not related to the presence of obvious growths of diatoms and blue green algae, which occurred abundantly in one group of samples but not in the other.

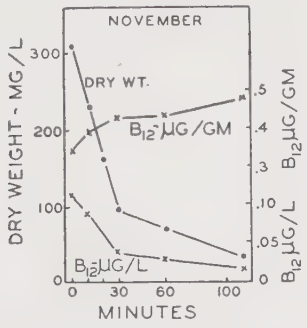

FIG. 4. Dry weight and vitamin B_{12} in suspended particles filtered from the upper 3.5-cm layer of sea water allowed to settle in one gallon jugs for different periods of time. Water was obtained at ebb tide from the Duplin River at Marsh Landing on November 28, 1955.

TABLE 3. *Vitamin B_{12} in three types of marsh mud collected October 26, 1955, Sapelo Island, Georgia*

Location	Marsh Type	Vitamin B_{12} µg/g
Jack Creek	Low Marsh	0.720
		0.520
		0.770
	Average	0.670
Jack Creek	Middle Marsh	0.870
		0.700
		0.700
	Average	0.757
Barn Creek	High Marsh	0.670
		0.700
		0.720
	Average	0.697

It should be pointed out that these two sets of data (Table 4) were obtained in assays made on materials which were not sulfite-treated. Further studies revealed that these data may be multiplied by a factor of 3.8 in order to obtain figures comparable with assays made on sulfited samples of mud.

ENRICHMENT OF MUD AND WATER

By the techniques of enrichment culture, it is often possible to develop the latent potentiality of the microflora and fauna present in any ecological habitat. For the purpose of discovering whether the vitamin B_{12} content of natural sea water and mud samples could be altered by enrichment, four samples of a low marsh mud and four samples of water from the Duplin River were enriched by addition of the following quantities per liter of sea water: peptone, 1.0 g; glucose, 1.0 g; K_2HPO_4, 0.025 g; KH_2PO_4, 0.025 g; yeast extract, 0.05 g; Wilson's liver fraction L, 0.05 g; and $FeCl_3$, 0.005 g. Approximately thirty milligrams of mud were weighed and added to 50 ml of enriched sea water medium for the purpose of developing the mixed population in these samples. Similar samples of mud and solids filtered from the water were assayed at the start of the enrichment period. The solids present in the enriched samples, supporting growth of micro-

TABLE 4. *Vitamin B_{12} in mud covered with algae and not so covered, August 26, 1955*

These samples were assayed without sulfite treatment; multiply by 3.8 to obtain values comparable with sulfited assays. B_{12} expressed as μg/gram of dried mud.

Location	With Algae	Without Algae
Jack Creek	60	53
"	61	60
"	58	62
"	100	90
"	80	80
"	77	82
"	68	66
West Fork, Duplin River	65	61
"	76	60
"	77	106
"	75	100
"	72	75
Average	72.4	74.5

TABLE 5. *Increase of vitamin B_{12} in enriched marsh mud and estuarine water, collected August 26, 1955, Sapelo Island, Georgia*

Source of mud	Before enrichment		After enrichment		Increase of B_{12} (D/B)
	mg of mud/ml (A)	B_{12} μg/L (B)	Dry weight mg/L (C)	B_{12} μg/L (D)	
South Basin	0.57	0.34	1.29	10.0	29.4
South Basin	0.64	0.21	1.21	5.5	25.7
South Basin	0.78	0.26	1.04	7.5	28.8
Barn Creek	0.63	0.28	1.05	3.4	12.1
Source of water	**mg of solids /L (A)**	**B_{12} μg/L (B)**	**Solids mg/L (C)**	**B_{12} μg/L (D)**	**Increase of B_{12} (D/B)**
Duplin River, surface	25.8	0.014	620	0.38	26.6
Duplin River, 5 meters	40.0	0.020	806	0.26	13.0
Duplin River, surface	15.8	0.007	107	0.30	42.2
Duplin River, 6 meters	50.6	0.020	718	0.50	25.0

organisms, were assayed after three days. The data in Table 5 show that the amount of suspended solids increased as a result of enrichment, and that the vitamin B_{12} content of the samples increased by as much as 12.1 to 42.2 fold. It is probable that this increase of vitamin B_{12} is a result of the great growth of bacteria which occurred in these enriched sea water media.

VITAMIN B_{12} IN PURE CULTURES

One hundred and thirty isolates of marine bacteria were obtained from marine mud and sea water by the agar plating technique. A selected group of these were grown in sea water enriched with extracts of *Spartina* grass. Assays were made, with the *E. coli* agar plate method (Sebrell and Harris 1954), on the medium and on the whole culture after three days of growth. It was found that appreciable amounts of vitamin B_{12} were produced by many of these bacteria, ranging up to about 0.150 μg per ml. It appears, therefore, that the grass extract can support growth of many marine bacteria collected in the region around Sapelo Island, Georgia, and that some of these bacteria are capable of producing significant amounts of vitamin B_{12}.

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The Effect of Removal of Fixed Percentages of the Newborn on Size and Variability in Populations of *Daphnia pulicaria* (Forbes)

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ABSTRACT

Populations of *Daphnia pulicaria* were maintained under laboratory conditions of constant food supply and temperature. Varying percentages of the newborn were removed from the populations at four-day intervals. Mean size of the residual populations decreased with increasing removal rate, while yield and yield per individual increased. Mean differences between the number of animals present at successive censuses after removal of the newborn decreased with removal rate while mean differences between successive yields increased. The sum of mean differences in residual population and yield was a constant, independent of removal rate. That is, total variability in the population-removal system was not changed by removal rate, although the variability was divided between yield and residual population. The ratio of yield variability to population variability was dependent on removal rate and on the fact that only newborn animals were removed, but was independent of food supply and temperature differences between populations. This ratio also may be independent of the physiological peculiarities of *Daphnia*. Median life expectancy of the survivors was increased 13–15 days when the removal rate was increased from 25% to 90% of the newborn. The median life expectancy with 90% removal was 32 to 36 days.

INTRODUCTION

While there have been many studies of population growth in the laboratory, until recently there have been no published laboratory experiments on exploitation or predation of populations in the laboratory. The present experiments were therefore started in March 1954 to determine experimentally the effect of removal of varying percentages of newborn animals from populations of *Daphnia pulicaria*. It was hoped that the effect of predation on these populations could be determined in the laboratory without the obscuring factor of environmental change.

Concurrently and independently two similar studies were being conducted, one by Nicholson (1954a) using *Lucilia cuprina* and one by Watt (1955) using *Tribolium confusum*. Due to the taxonomic and ecological disparities between the organisms used, these studies are complementary and will be compared in greater detail below.

The role of theoretical and experimental models in fishery exploitation theory

In the process of exploiting any non-domesticated population of organisms, man assumes the role of a predator. He differs from a non-human predator in his ability to attempt to calculate his strategy of predation so as to maximize both his profit and the likelihood that the exploited resources will persist from year to year. These maximizations may be mutually incompatible in particular cases, but as a rule both are considered in designing an exploitation program. Extra-biological factors often influence exploitation procedure. These may include such things as the aesthetic or political opinions of the consuming public or mechanical problems of packing or transportation.

It is obvious therefore that no one exploitation theory can be considered universally applicable. It can be demanded, however, that any theory purporting to deal with the purely biological aspects of an exploitation situation must be powerful enough to account for at least the minimum of biological complexity that might be expected to arise in the natural world.

In particular, all exploited populations, to our knowledge, are composed of multicellular organisms. It is only recently that models which acknowledge the difference between individual animals of a population of metazoans have been constructed. The

work of Ricker (1954b), Beverton (1953), Slobodkin (1953b), and Watt (1955) are typical examples of these models.

Two of these models have been applied to laboratory or field data. Beverton has discussed the applicability of his model to the plaice fishery, and Dickie and McCracken (1955) have applied the same model to a flounder fishery. Ricker has applied his model to the data of Pratt (1943) on laboratory populations of *Daphnia magna*. While Beverton's model has been used for prediction, to date the predictions have not been tested. Ricker's analysis of Pratt's *Daphnia* data produced a graph of theoretical population size against time which was very similar to the actual observations. Both of these models make empirical assumptions which detract from their generality. Beverton assumes a constant recruitment of new stock and Ricker assumes that mortality is independent of population density after sexual maturity.

While the models of Slobodkin and Watt are almost completely general, they also involve such a large number of fitted constants as to be inapplicable to any real situation. What is required is a model or a set of generalities which combines the applicability of Beverton and Ricker with the flexibility of the other two.

This study has been undertaken in the hope that empirical conclusions derived from an extremely simplified system may facilitate formation of more satisfactory theories of exploitation, or at least be of help in determining the minimum level of complexity of even the simplest of exploitation systems.

Population dynamics of Daphnia

Daphnias are particularly convenient organisms for population studies. They are normally parthenogenetic, so that both genetic heterogeneity and complex sex behaviour are absent. Since they are aquatic filter feeders the geometric complexity of the culture vessels is minimized. The animals of a population interact with each other only through their effect on the food supply, thereby eliminating social complexity from the system.

Normal population growth in *Daphnia* has been examined in *Daphnia magna* (Pratt 1943), *D. pulicaria* (Frank 1952) and *D. obtusa* (Slobodkin 1954). The pattern derived from these studies has not been reexamined in the present experiments but there is no reason to doubt its applicability.

Briefly outlining the normal population pattern of *Daphnia*, mean population size is determined exclusively by the rate of feeding in any constant set of physical conditions. There is no evidence at all of any metabolites, or any other interaction between animals except competition for food (Slobodkin 1954). The feeding rate varies with the size of the individuals (Ryther 1954) as do the food requirements for survival. The growth rate of animals of any particular age depends on their food supply (Rodina 1946) and on their previous nutritional history (Slobodkin 1954). The same statements apply to the reproductive rate. Detailed quantitative interactions of age, growth, reproduction, previous history, and food supply have not yet been worked out.

Due to the differences between the individual animals in the population, oscillations in population size are found even in the most carefully controlled environments. Under certain conditions of temperature these oscillations eventually disappear and a population equilibrium occurs in which the total number of animals, reproductive rates, growth rates, and size-frequency distribution remain invariant with time (Pratt 1943, Slobodkin 1954).

Fluctuations occur in the present experiments, which may be either internal or determined by environmental changes. The cause of the fluctuations is irrelevant to the conclusions to be drawn.

Acknowledgements

Dr. John L. Brooks kindly identified the *Daphnia pulicaria*. Mr. Robert Paterson provided the original stock of *Chlamydomonas*.

Mrs. Shanti Latta Kanungo and Mr. Thomas Parker helped with the population counts.

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TECHNIQUE

The procedure followed in these experiments was a modification of that reported by Slobodkin (1954).

Populations were started with from ten to thirty adult animals in 50 cc of conditioned water. The animals were counted, dead were removed, the water was changed, and the appropriate number of living animals was removed every fourth day. The populations were fed a measured amount of *Chlamydomonas Reinhardi* either every other day or every fourth day. At the time of counting the populations were divided into four arbitrary and subjective size categories: young, small adolescent, large adolescent, and adult. The number of eggs in the brood chamber of fertile females was counted.

Fixed percentages of the newborn animals were removed. In cases where the number of animals to be removed was fractional the next lowest whole number of animals was removed. The removal percentages listed are therefore maximum values, so that "not more than 25% removal" should be read for "25% removal" and similarly for the other removal rates.

The water used in these experiments was Ann Arbor tap water which was stored in a large concrete tank containing attached algae, clams, and several small fish. The water was aerated and lighted continuously.

The experimental containers were soft glass, wide-mouthed bottles of approximately 130 cc capacity and 6 cm outside diameter. Glassware was washed in the way indicated in Slobodkin (1954) with the added precaution of rinsing with de-mineralized distilled water.

The algae were raised on sterile agar plates. The algal medium is indicated in Table 2.

The algae were suspended in conditioned water and the concentration of the suspension was measured with a Klett photometer using a red (no. 64) filter. An amount of this suspension sufficient to give a Klett reading of 5 in 50 cc of medium was added to the *Daphnia* populations at each feeding. For example, one cc of a suspension with an initial Klett reading of 250 would constitute one feeding.

All the populations were kept in dark incubators except during the actual counts.

There were three experimental series of populations. One, kept at 15°C and fed every other day will be referred to as H-15. One, kept at 19°C and fed every other day will be referred to as H-19.

TABLE 1. *Dates of initiation and termination of experimental populations, and initial number of animals (adult females) in the populations*

The populations of series H-15 have not been listed separately in the table. The populations of this series were maintained at 0%, 25%, 50%, 75%, and 90% fishing rates and were all initiated with 20 adult animals on June 29, 1954, and were terminated on March 31, 1955.

Series	Fishing rate	Date started	Initial size
L-19	0%	March 18, 1954	20
All terminated	25%	March 16, 1954	15
March 29, 1955,	33%	October 4, 1954	20
except 66% &	50%	January 12, 1955	30
33%	66%	October 4, 1954	20
	75%	July 20, 1954	20
	90%	March 14, 1954	20
H-19	0%	July 11, 1954	52
All terminated	25%	October 5, 1954	20
March 30, 1955	50%	September 11, 1954	30
	75%	July 11, 1954	20
	90%	July 11, 1954	20

TABLE 2. *Nutrient agar for growing Chlamydomonas*

*Beyerinck's solution	100 cc
Soil extract	50 cc
Distilled, demineralized water	850 cc
3 drops 1% aqueous $FeCl_3$	
Agar	15 g

*Beyerinck's solution

Distilled, demineralized water	1000 cc
NH_4NO_3	0.5 g
K_2HPO_4	0.2 g
$MgSO_4 \cdot 7H_2O$	0.2 g
$CaCl_2 \cdot 2H_2O$	0.1 g

One, kept at 19°C and fed every fourth day will be referred to as L-19.

In all three series populations were maintained at removal rates of 0, 25, 50, 75 and 90 per cent of the newborn. In series L-19, populations were also maintained at removal rates of 33 and 66 per cent of the newborn for brief periods.

The number of newborn animals in a population was computed by taking the sum of the living and dead animals found in the container at any particular count and subtracting from this the number of living animals returned to the container after the previous count.

The fishing procedure consisted of multiplying the number of newborn by the appropriate fishing rate, rounding off the product to the next lowest whole number and removing the appropriate number of animals at random from the newborn. The term "random" is used in a limited sense. For example, if twenty-five per cent of the newborn were to be removed from a particular population, the individual doing the counting placed three successive animals in the new culture vessel and discarded the fourth. The animals were taken in order of catching with a medicine dropper.

Fairly often the number of animals in the "young" size-category was not equal to the calculated number of newborn. If the number of young animals was in excess of the calculated number of newborn it was assumed that the growth rate of the newborn animals remaining after the previous census was so low as to prevent them from growing into the "small adolescent" size-category in the interval between counts. If the number of young animals was less than the number of newborn we assumed that the growth rate of the newborn animals produced since the last census had been sufficiently rapid to permit them to grow into the small adolescent size-category in the interval between their birth and their first census.

In the first case the number of animals removed from the young size-category was the number derived from the product of the fishing rate and the calculated number of newborn. That is, in a twenty-five per cent fished population with four newborn animals, only one animal would be removed regardless of the number of young animals found.

In the second case the appropriate percentage would be removed from the young category and the remainder removed from the small adolescents. On rare occasions the calculated number of newborn exceeded the total number of young and small adolescents together, in which case large adolescent animals were also removed. In no case did an animal grow into the adult category between counts.

There are two sources of error in this procedure: 1. fractional animals were left to the population; 2. any animals that died and decomposed completely between counts would tend to increase the estimated number of newborn. These two sources of error counteract each other to some extent. The first is probably not of major importance. The second is probably not significant at the temperatures used. Newborn *Daphnia* show characteristic oil droplets which act as a check on the calculated number of newborn to some degree. In short, there is an unknown amount of error in the procedure, but the mutual consistency of the results indicates that this error is not appreciable.

The percentage of the animals which were to be removed from any population was fixed at the initiation of that population and was not changed during the life of the population.

The present experiments more closely simulate natural predation than commercial fishing since we removed newborn animals rather than adults. At the present stage of experimental analysis it seemed advisable to deal with a system that showed promise of being extremely simple. Further experiments, in which adult animals are removed, are now in progress.

EXPERIMENTAL RESULTS

Mean population size and yield

While temporal variation is of particular interest in these studies, it is simplest to

first analyze the values of yield and population size taken as averages over the entire history of the individual populations. These means are distorted by the fact that the initial population size was independent of the fishing rates but, as will be demonstrated below, the effect of initial population composition is insignificant after sufficient time has elapsed.

We will use the term "population size" or "size" to mean the number of animals present in the population after the completion of the counting and fishing procedure. The term "total standing crop" will be used to refer to the number of animals present in the experimental containers prior to fishing, following the usage of Watt (1955).

In all three experimental series, mean population size decreased with fishing intensity (Fig. 1). In general the decrease was non-linear. This is particularly well demonstrated in series H-15. The departures from a smooth non-linear decrease shown by series H-19 and L-15 are artifacts caused by premature termination of the experiments. In particular, the mean size of the 0% fished population of H-19 is excessively high as are the means of the 25% and 0% fished populations of L-19.

Average yield increased with fishing rate, with a consistent maximum at 90% fishing. The average yield over infinite time of a population fished at a rate of 100% is obviously zero, so that the yield at 100% fishing has been assigned a value of zero in all three series.

The yield from any population is the increase above the requirements for population maintenance, expressed either as growth or reproduction, multiplied by the total number of individuals in the population. Yield per individual was accordingly computed by dividing the mean yield of each population by mean population size. This is indicated in Figure 1. Since the major portion of the yield was in animals of uniform size, biomass yield and numerical yield are directly proportional. The yield per individual is a smooth, nonlinearly increasing function of fishing rate in all three series.

Variability in total population size

In Figures 2, 3, and 4 are indicated total population size as a function of time in all three series. There is some fluctuation in size in every population. At the moment it is impossible to state precisely what proportion of the total variability is due to slight alterations from time to time in the environment. The degree of correlation between different populations would indicate some environmental variability. Comparison of these figures with other published graphs of *Daphnia* populations indicates that at least some of the fluctuation is due to the internal population adjustment mechanisms outlined in the introduction and discussed in detail elsewhere (Slobodkin 1954).

Size-frequency distribution, fishing rate, and stability

Stability characteristics have been partially defined for natural communities by MacArthur (1955). The interaction between stability and reproductive patterns in a restricted single species population model has been discussed by Ricker (1954a, b). Existence criteria for population equilibrium, implicitly containing necessary but not sufficient conditions for single species population stability, have been developed for a more general model by Slobodkin (1955). It is now possible to demonstrate an experimental correlation between population stability and size-frequency distribution.

In Figures 5, 6, and 7 the total number of animals in each of the four size-categories has been summed over the entire census period for each population.

In series H-15 (Fig. 7) all of the populations were maintained for an identical length of time so that the absolute heights of the histogram bars are comparable. It will be noted that in this series the number of animals in each category decreases with fishing intensity, demonstrating that the reduction of population size with fishing intensity is an actual reduction in biomass and not merely a decrease in numbers.

In all three series the relative number of

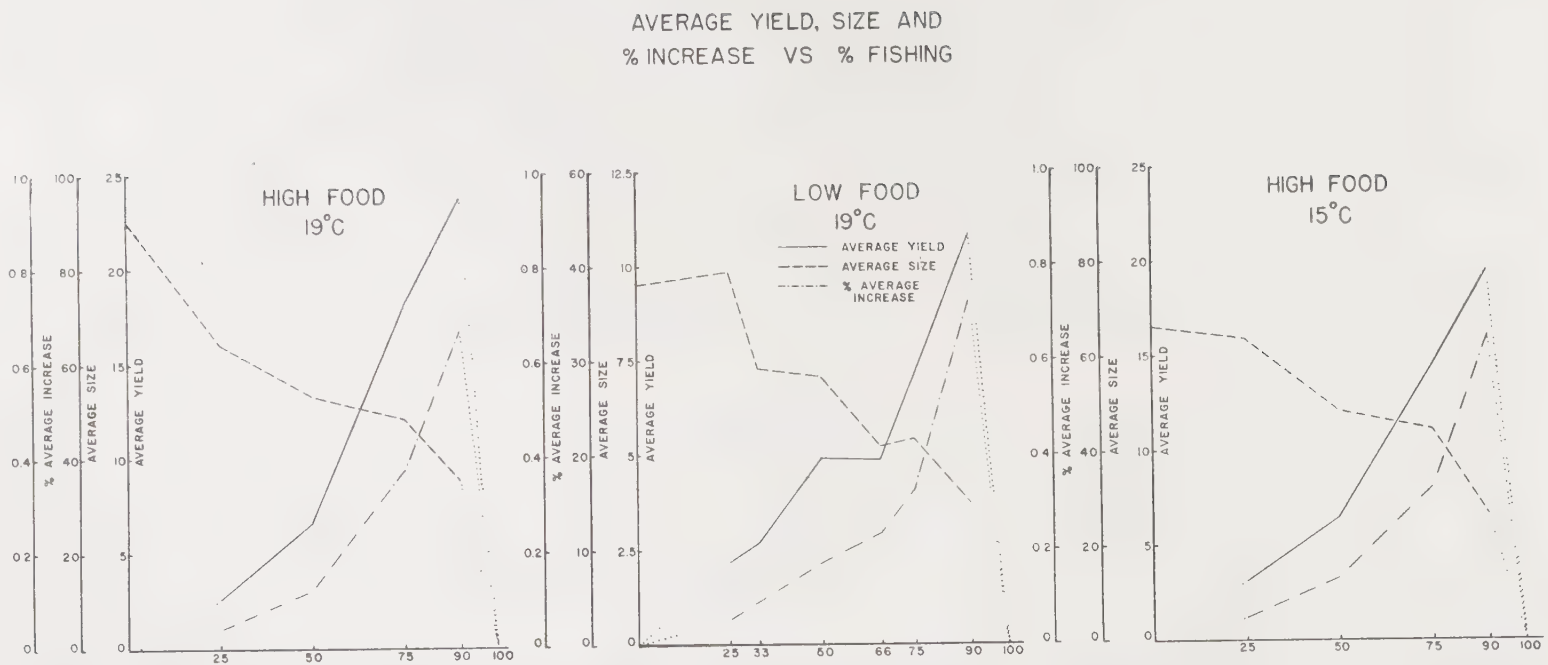

FIG. 1. Mean size of populations after fishing (- - - -), mean yield per day (— — —), and yield per individual per day (-·-·-) for the three series of experiments. The data for Series H-15 (far right) are probably more accurate than those of the other two series.

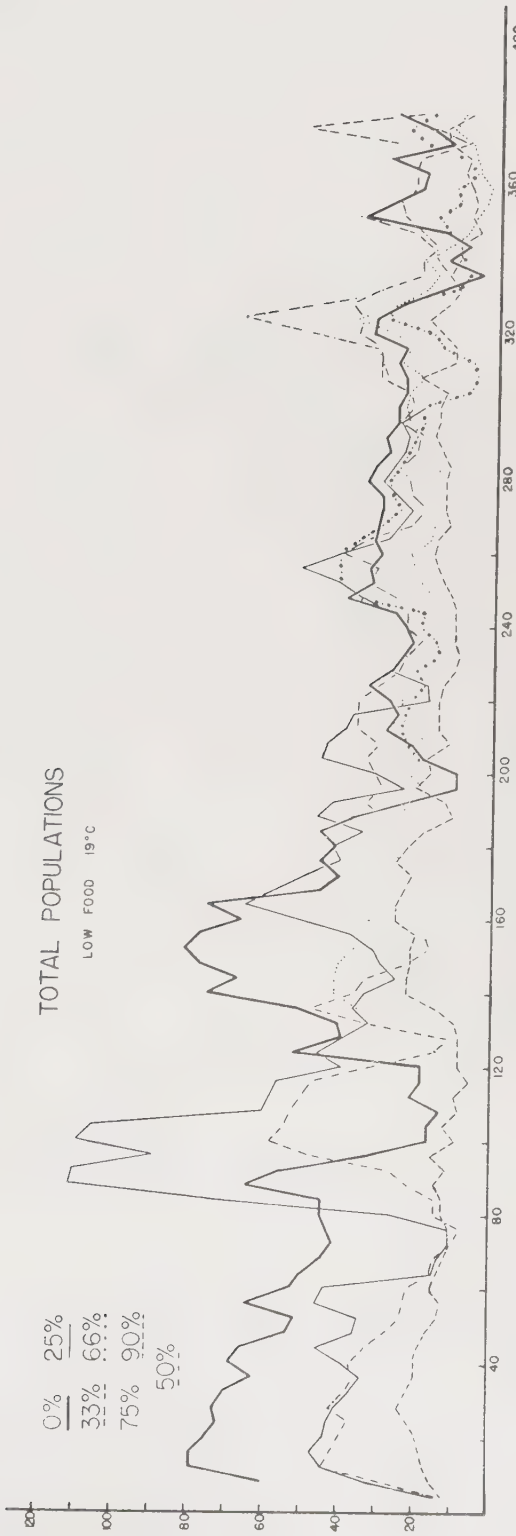

FIG. 2. Number of animals remaining in the populations after fishing (i.e. "population size") in the seven populations of series L-19, plotted against time in days.

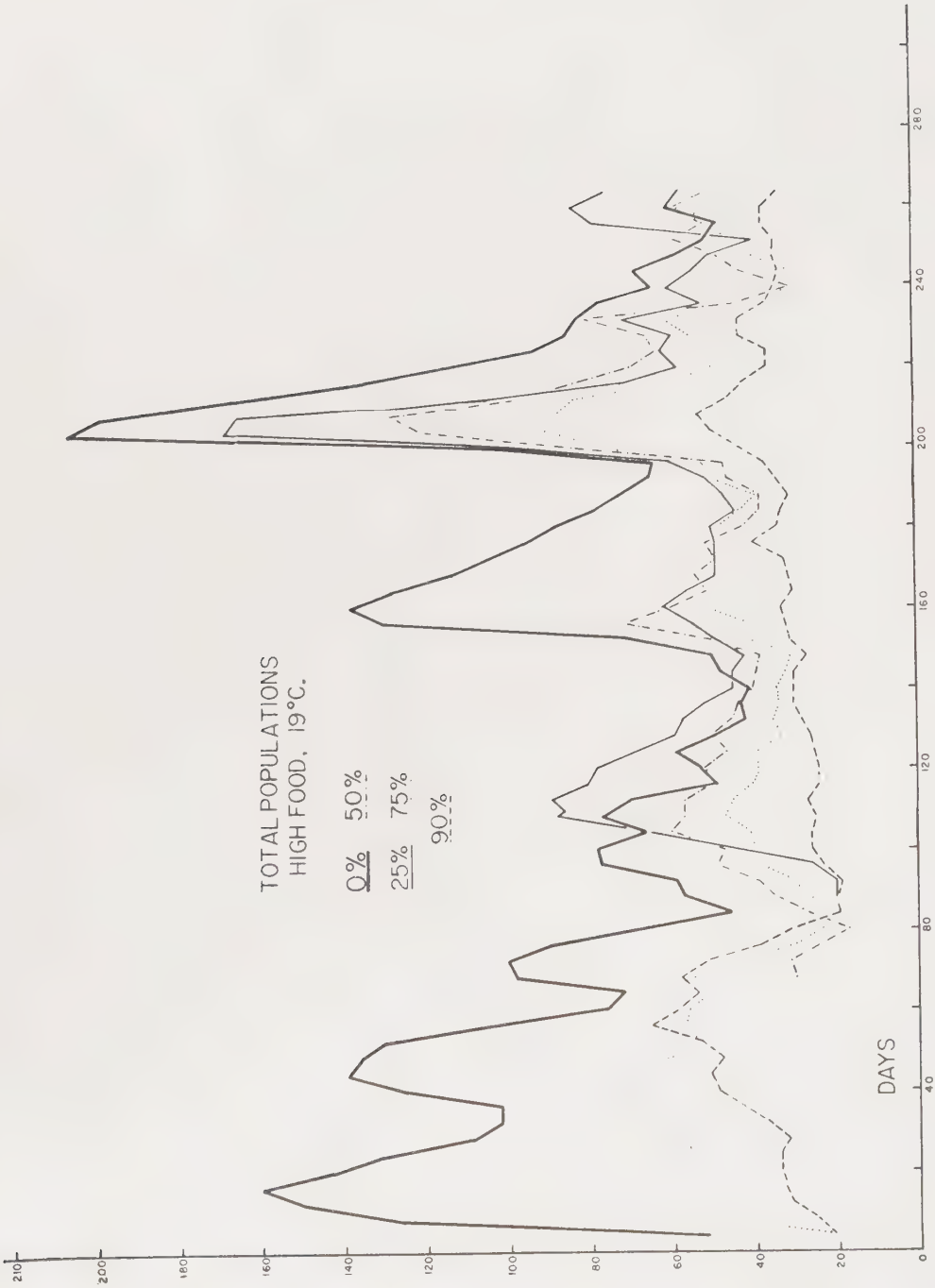

FIG. 3. Population size in the five populations of series H-19, plotted against time in days.

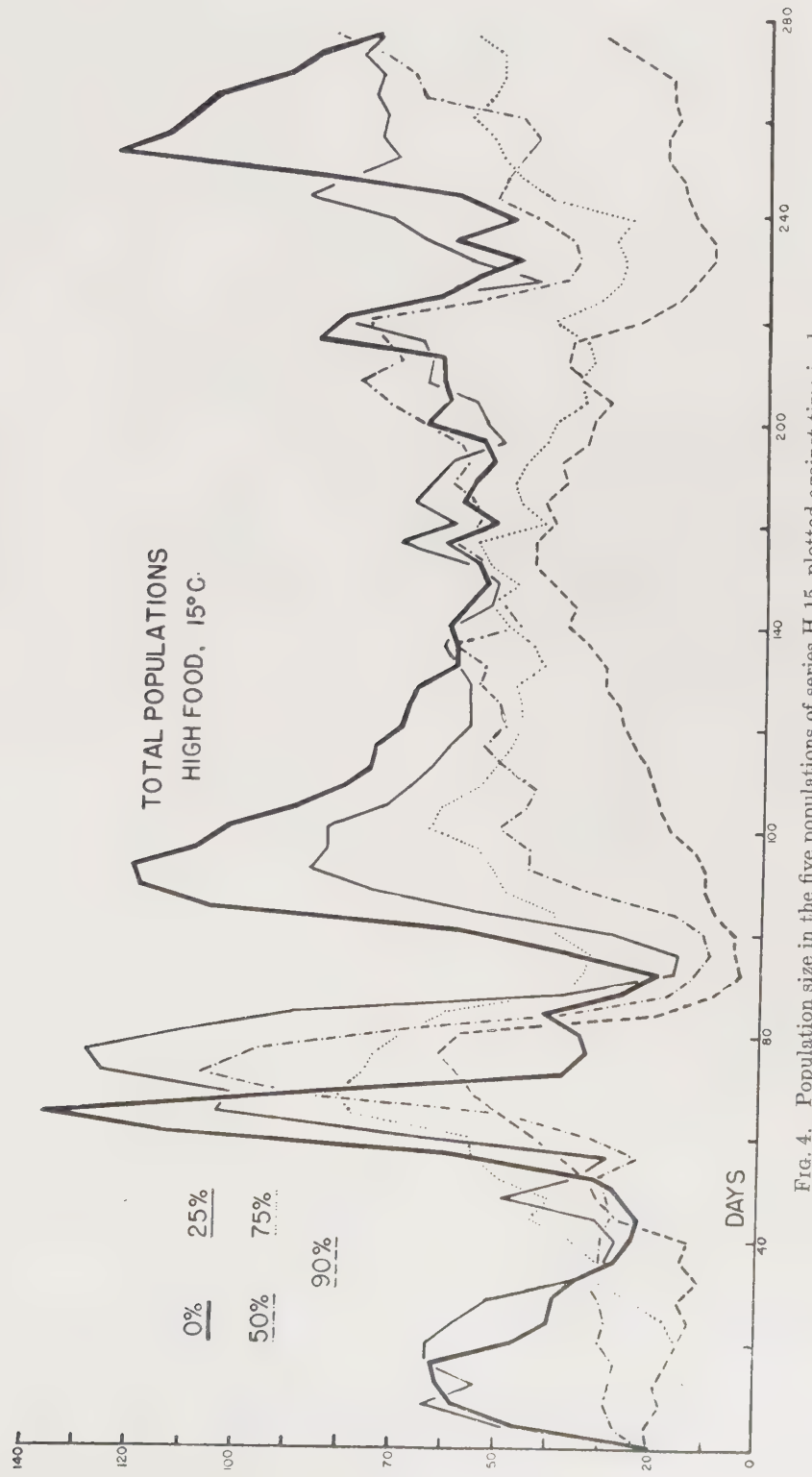

FIG. 4. Population size in the five populations of series H-15, plotted against time in days.

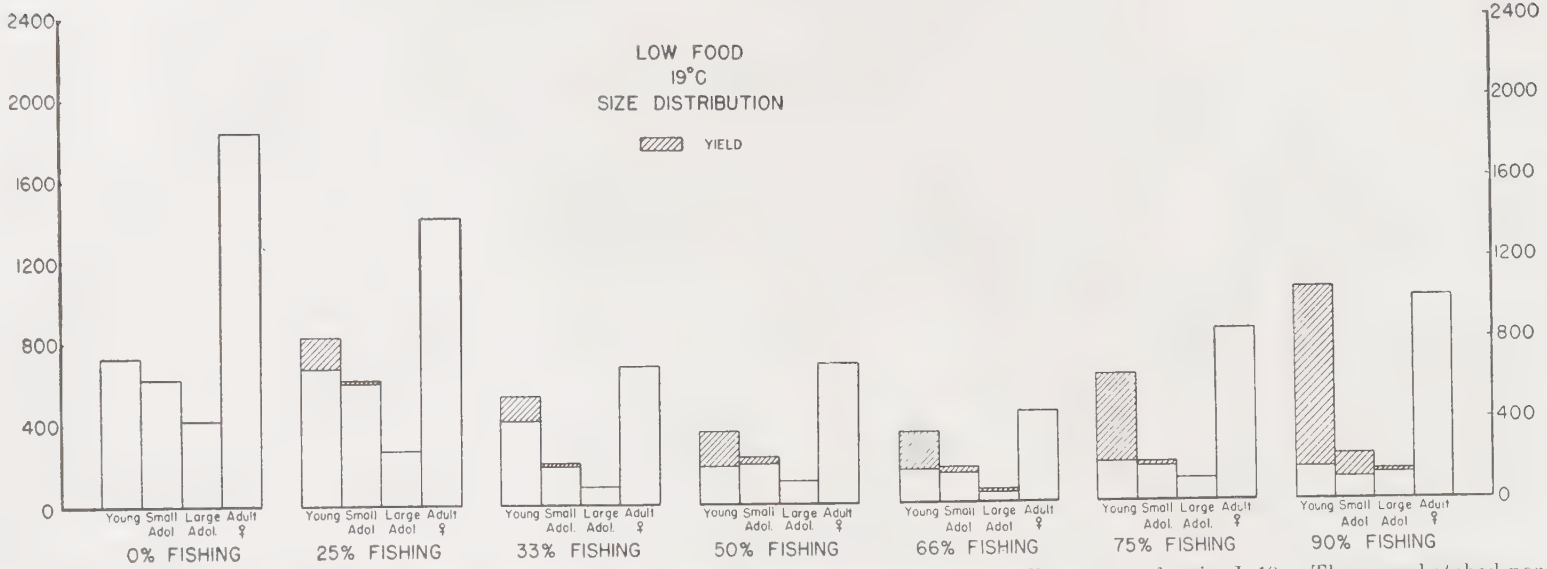

FIG. 5. Cumulative totals of the number of animals in each of the four size categories during all censuses of series L-19. The cross-hatched portions of the bars represent the animals removed during fishing.

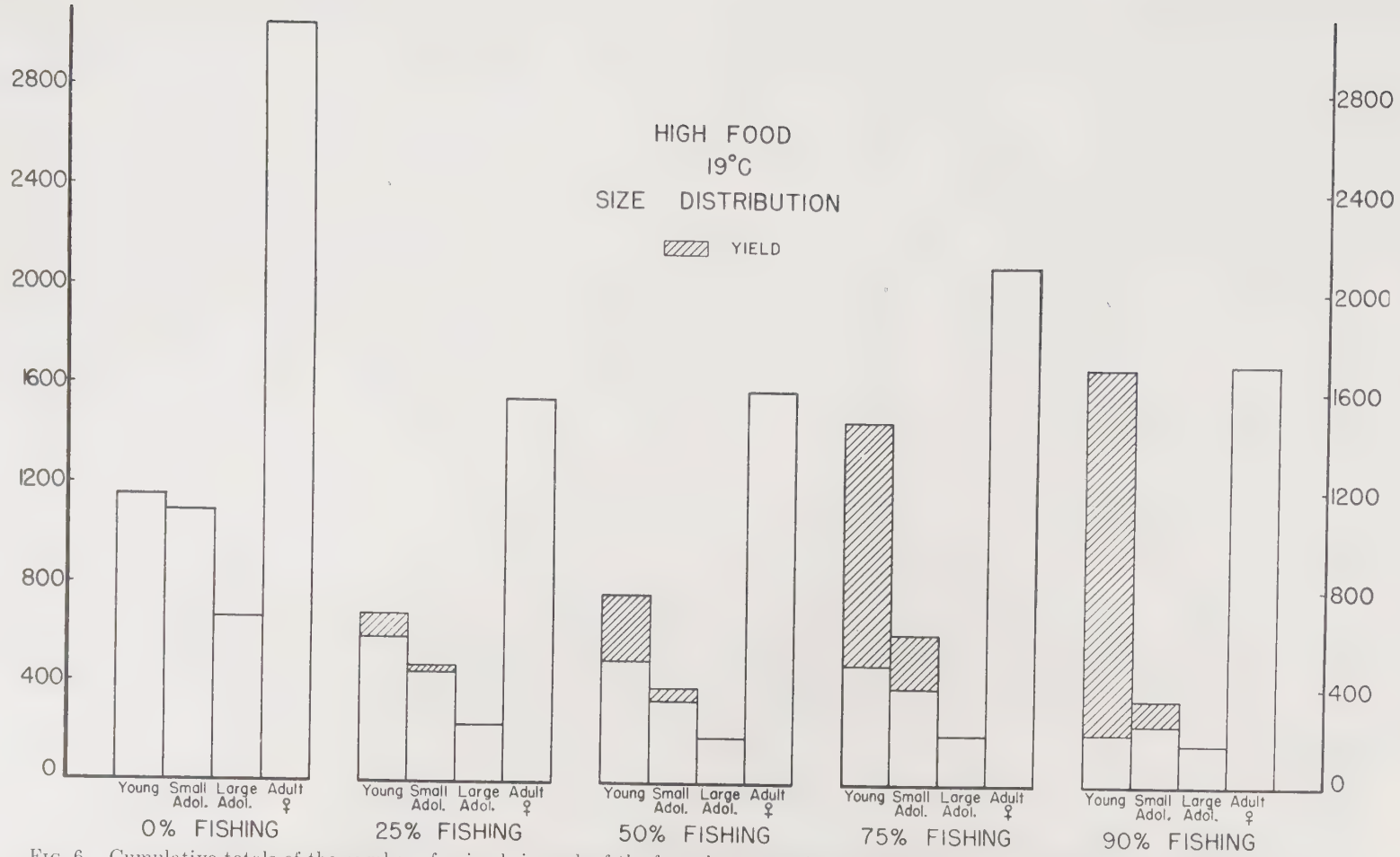

FIG. 6. Cumulative totals of the number of animals in each of the four size categories during all censuses of series H-19. The cross-hatched portions of the bars represent the animals removed during fishing.

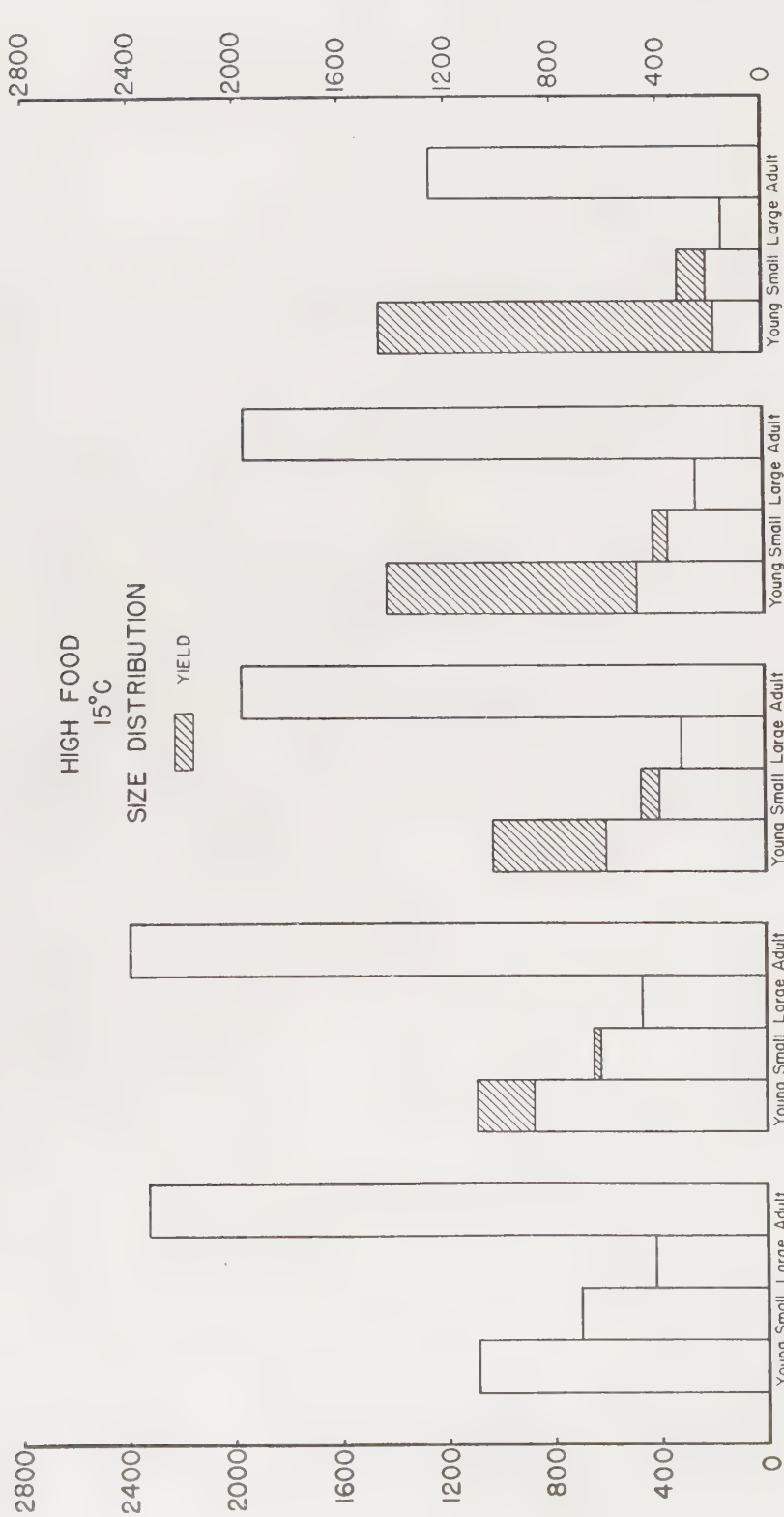

FIG. 7. Cumulative totals of the number of animals in each of the four size-categories during all censuses of series H-15. The number of censuses was identical in all the populations of this series. The cross-hatched portions of the bars represent the animals removed during fishing.

animals in the three smaller size-categories changes in a regular way with fishing intensity. With 0% fishing there is a preponderance of young animals and a minimum of large adolescent animals. It must be emphasized that these terms are size categories and not age categories. It is impossible to determine the age of individual animals in these populations once they are older than four days. As fishing intensity increases, the disparity between the number of animals in the three smaller size-categories decreases until at 90% fishing the number in these three categories is approximately equal.

It can be shown theoretically that given an animal with a rectangular survivorship curve (Deevey 1947), in which mortality affects primarily old individuals and is concentrated in a narrow age span, the relative number of animals in any size-category in an equilibrium population is inversely proportional to the first derivative of the growth curve of an individual in that size-category. That is, the faster the animals grow through any size range, the smaller the number of animals that will be found in that size range at population equilibrium. Incidentally, the number of animals in any two equal age-intervals of an equilibrium population with a rectangular survivorship curve is identical.

Pratt (1943) and Anderson and Jenkins (1942) have demonstrated that there is very little mortality prior to the adult stage in *Daphnia magna*, and Frank (1952) has repeated these observations for *Daphnia pulicaria* (not, however, the same strain as that used in these experiments). It seems safe to assume the mortality pattern of the present strain of *Daphnia pulicaria* to be similar to that found by these workers.

It has been shown by Anderson, Lumer, and Zupancic (1937) and Tonolli (1947) that the growth curve of an individual *Daphnia* consists of a decelerating increase approaching an upper asymptote, with a remarkable short accelerating phase at the young end.

It is to be expected, therefore, that the size distribution in equilibrium populations of *Daphnia pulicaria* should be approximately the same as that found in the 90% fished populations. Similar size distributions have been found in equilibrated populations of *Daphnia magna* (unpublished data of David Pratt) and *Daphnia obtusa* (Slobodkin 1954). The size-frequency distributions found at low fishing intensities are clearly incompatible with population equilibrium. We might expect that stability of the populations should be proportional to the fishing rate. This expectation can be confirmed intuitively by examining Figures 2, 3, and 4.

Food consumption, fishing rate, and stability

Considering the *Daphnia* populations as simple feedback systems (Wiener 1948), the degree of instability is proportional to the time lag in the reactions of the populations to alterations of the environment. The greater the time lag between the moment an adjustment to environmental alteration is started by a population and the completion of that adjustment, the more unstable the population.

There are three major lag effects inherent in almost all metazoa. An animal born at one instant dies at some subsequent instant. An animal born at one instant begins to reproduce at some subsequent instant. An animal born at one instant will make a certain contribution to population density at that instant, and this contribution to population density may be expected to change as the animal grows older. The first two of these sources of instability are essentially immune to modification by fishing. The third can be completely eliminated by suitable exploitation.

If the total contribution to population density of a group of animals immediately after their birth is x, which is just sufficient to restore population density equilibrium, and the total contribution to population density by these animals at the age of maximum density contribution is $x + y$, then the portion of their density contribution which will contribute to population instability is y. Removal of $\frac{y}{x + y}$ of the

animals at birth will minimize this source of oscillation.

From the life table data of Pratt (1943), the weight-increase data of Edmondson (1955), the feeding rate observations of Ryther (1954), and the fact that *Daphnia* populations are limited solely by food supply (Slobodkin 1954), it is possible to estimate that the density contribution, i.e. the food consuming capacity, of a group of *Daphnia* at birth is from one-sixth to one-tenth the density contribution of the same group at maturity, assuming complete survival of the members of the group to maturity. The minimization of population fluctuations at 90% fishing rates, which has been found in these experiments, would be expected on the basis of this analysis.

It is of interest that fluctuations were not damped to the same degree by 90% fishing in the experiments of Nicholson (1954a). He was removing adult flies from populations of *Lucilia cuprina*. These flies had already made their chief contribution to population density.

It seems possible that the same arguments might apply to the exploitation of any density-dependent natural population. In general, if the minimum marketable size consists of a group of animals whose total contribution to population density is x, and the density contribution of the same group at maturity is $x + y$, removal of the animals at the rate of $\frac{y}{x + y}$ will minimize fluctuations from this source.

This assumes no inherent incompatibility between satisfying this condition and satisfying the equilibrium condition indicated above; that the relative number of animals in any size category of an equilibrium population is proportional to the inverse of the growth rate of an individual of that population at any particular size, multiplied by a correction term computed for each size as the product of the survival rates of all smaller size categories.

The partitioning of variability between yield and population size

While it is intuitively apparent that the heavily fished populations are less variable in size than the less heavily fished populations (Figs. 2, 3, and 4), it seems desirable to quantify this variability in some way. Recent work and controversy have amply demonstrated the dangers of most of the methods used to search for "cycles", periodicities, or even variability in population data (Hewitt 1954). We have nevertheless attempted to get a measure of total variability by summing the differences between successive counts regardless of sign for each population.

Variability in this sense has been computed for both total standing crop and population size and, since the length of time of observation varied from population to population, the total variability has been divided by the number of censuses giving mean change per census for each population (Table 3).

The total standing crop variability represents the sum of the variability in population size and in yield. If the total variability of the population-yield system was being changed by fishing we would expect some significant relation between total standing crop variability and fishing rate. It can be seen from Figure 8 that there is no significant relation at all.

TABLE 3. *Mean total standing crop, yield, population size, and variability in total standing crop and in population size*

Population	Mean total standing crop	Mean population size	Mean yield per census	Variability in total standing crop	Variability in population size
H-19					
0%	90.833	90.833	0	14.892	14.892
25%	66.900	64.341	2.659	14.023	11.930
50%	66.449	59.898	6.551	13.714	9.020
75%	66.499	48.287	18.212	19.061	6.323
90%	59.272	35.530	23.742	17.108	3.369
H-15					
0%	66.072	66.072	0	11.809	11.809
25%	67.043	63.899	3.144	11.250	9.456
50%	55.115	48.666	6.449	10.544	6.926
75%	59.145	44.696	14.449	12.074	4.735
90%	45.782	26.289	19.493	14.265	3.691
L-19					
0%	38.032	38.032	0	6.731	6.731
25%	42.053	39.893	2.160	10.000	8.351
33%	31.751	29.063	2.688	9.583	6.521
50%	36.026	30.821	5.205	10.615	6.256
66%	25.773	20.909	4.864	7.222	4.022
75%	28.667	21.635	7.032	9.159	3.143
90%	25.663	14.874	10.789	10.347	2.295

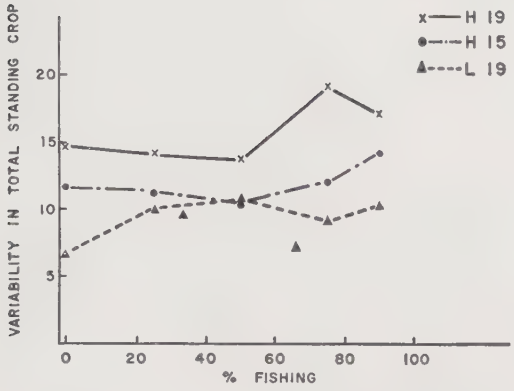

FIG. 8. Variability in total standing crop as a function of fishing rate. Variability is defined as the sum of the absolute differences between successive counts of total standing crop, divided by the number of censuses. The values at 33% and 66% removal are probably aberrant. There is no significant relation between total standing-crop variability and fishing rate.

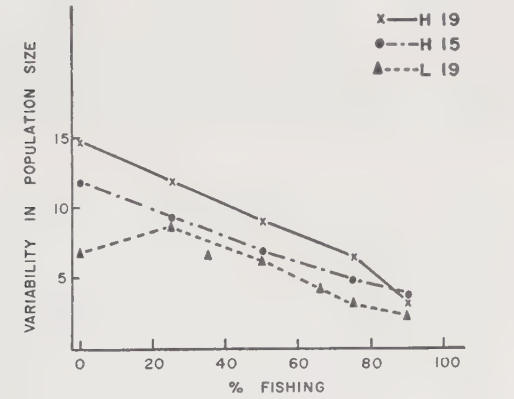

FIG. 9. Variability in population size as a function of fishing rate. Variability is defined as the sum of absolute differences between successive counts of population size (i.e. animals remaining after fishing) divided by the number of censuses. There is a significant decrease of population-size variability with increased fishing.

The decrease of population size variability shown in Figures 2, 3, and 4 is more clearly demonstrated in Figure 9 where variability in population size is plotted against fishing rate.

Variability in yield can be computed as the difference between total standing-crop variability and population-size variability. Yield variability has been plotted against fishing intensity in Figure 10, demonstrating the increase of yield variability with fishing intensity.

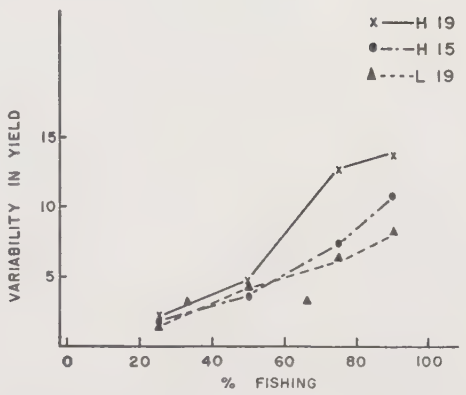

FIG. 10. Variability in yield, measured as the difference between total standing-crop variability and population-size variability, as a function of fishing rate. There is a significant increase of yield variability with fishing rate.

We conclude that fishing simply divides a fixed amount of total variability into two portions, one being assigned to the yield and the other to the population size. It is now necessary to find out what properties of the system determine the relative amounts of variability in the two components.

If we replace the fishing rate by $\frac{1-p}{p}$, where p is the percentage removal, and plot this against the ratio of yield variability to population variability, an equilateral hyperbola is produced (Fig. 11). The total range of calculated values for the coordinates of the focus of the hyperbola, computed as a, a, where

$$a = \sqrt{2\,\frac{(1-p)}{p}\,\frac{\text{yield variability}}{\text{population variability}}}$$

is 0.630 to 1.384 with a mean of 1.002 (Table 4). On a double log plot, Figure 11 is a straight line with slope of -1. The 5% confidence-limits of the slope are 0.86 and 1.18, by the Kendall sum method (Tukey 1950). This confirms the hyperbolic pattern of Figure 11.

Due to the close similarity between the three experimental series we can conclude that in *Daphnia pulicaria* the apportioning of total variability between yield and the residual population is independent of temperature and food supply.

This result is not particularly surprising, but it is surprising to find that the relation

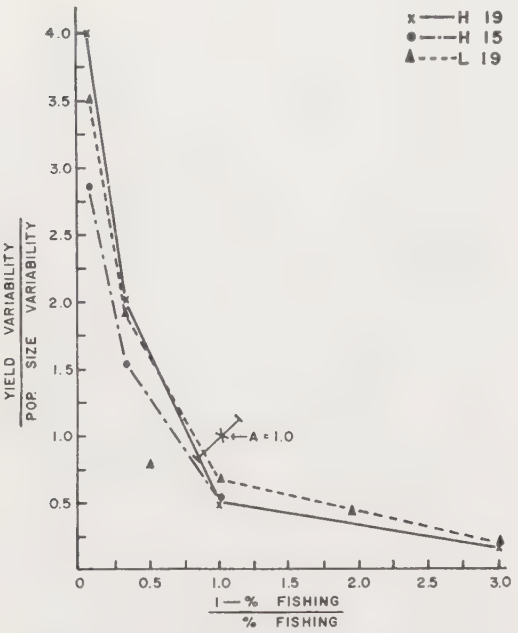

FIG. 11. The ratio of yield variability to population-size variability plotted against $\frac{1 - \text{fishing rate}}{\text{fishing rate}}$. The focus of this hyperbola is indicated by X at the point A = 1, 1. The total range of calculated values for the focus (with the exception of the data from population L-19 33%) is indicated by the diagonal line through X.

can be expressed by a simple hyperbola of unit focus. If the shape of Figure 11 were free to vary from species to species it would seem highly unlikely that the first species examined experimentally would be describable by such simple constants. We are tempted to conclude tentatively that the relation shown in Figure 11 is independent of the precise physiology of *Daphnia pulicaria*, and that it either would be found in all other species examined or that all species are divisible into a fairly small number of classes, for which the shape of the relation would vary from class to class but would be constant within each class. Implications of this conclusion are examined in the discussion.

We have already suggested that removal of newborn animals will probably have a greater tendency to lower population variability than would removal of older animals. If this suggestion is valid, then the shape of Figure 11 will depend on the

TABLE 4. *Calculated values of* a *for the hyperbolic relation shown in Figure 11*

$$x = \frac{\text{variability in yield}}{\text{variability in population size}};$$

$$y = \frac{1 - \text{fishing rate}}{\text{fishing rate}}; \quad a = \sqrt{2xy};$$

focus is at point a, a.

Population	x	xy	a
H-19 25%	0.175	0.525	1.025
50%	0.520	0.520	1.020
75%	2.015	0.665	1.153
90%	4.078	0.449	0.948
H-15 25%	0.190	0.570	1.068
50%	0.522	0.522	1.022
75%	1.550	0.512	1.012
90%	2.865	0.315	0.794
L-19 25%	0.198	0.594	1.090
33%	0.470	0.940	1.371*
50%	0.697	0.697	1.176
66%	0.796	0.398	0.892*
75%	1.914	0.632	1.124
90%	3.509	0.386	0.873

(* These values are from populations which had not yet reached stable mean size estimates and are probably not as trustworthy as the other values.)

fishing method. This conclusion is now being tested experimentally.

A hyperbola could be derived by assuming that variability in population size is proportional to population size. If our decrease of population variability were simply a reflection of decreased population size it would have as a consequence that variability per animal would itself be independent of population size. It is found however, by a graphical corner test (Bliss and Calhoun 1954: 197), that there is a significant increase of variability per animal (P less than .05) with increasing population size (Fig. 12). This confirms our previous analysis and specifically denies the contention that our observed reduction of variability with increased fishing was merely an effect of reducing total population size.

Life expectancy as a function of fishing intensity

If our argument on the relation between stability and size-frequency is valid, we

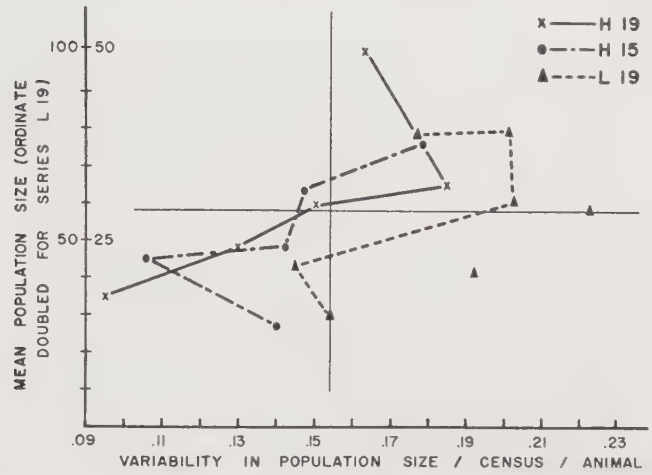

FIG. 12. The relation between mean population size and variability in population size per animal per census, demonstrating that the reduction of population-size variability at high fishing intensities was not simply due to a decreased population size. Horizontal and vertical lines have been drawn through the median points.

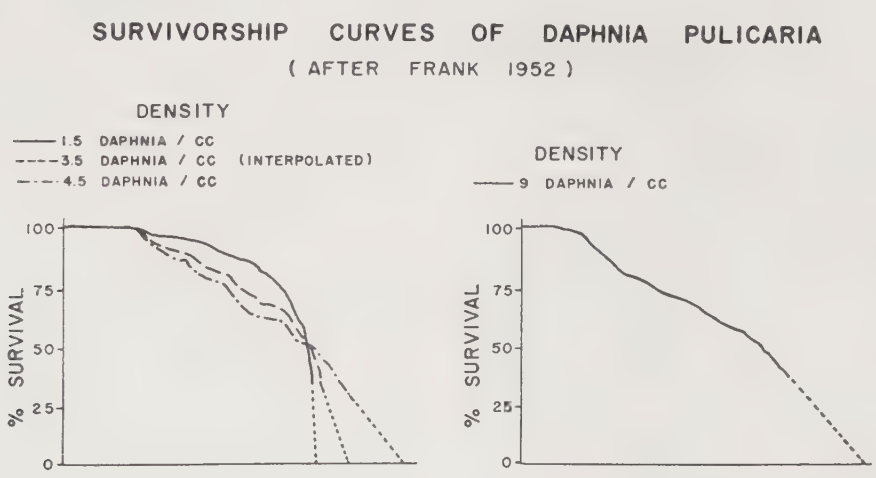

FIG. 13. Survivorship curves for *Daphnia pulicaria*, adapted from Frank (1952). The terminal portions of each curve are extrapolations. The survivorship curve for population density 3.5 has been interpolated.

should be able to demonstrate that the shape of the *Daphnia pulicaria* survivorship curve does not vary excessively with changes in population density. We can estimate the shape change by determining the ratio between mean and median life expectancies at the various population levels. Median life expectancy can be calculated from our data, while mean life expectancy can be determined by combining our data with the survivorship data of Frank (1952).

Knowing the mean size of a population which is neither increasing nor decreasing without bounds and knowing the mean rate at which the animals of that population are being replaced, it is possible to determine the median life expectancy of animals in that population, assuming that the replacement rate is effectively constant with time. The computation is a simple iterative process in which the replacement rate is computed as the quotient of mean number of animals entering the population per unit time divided by mean population size. This replacement percentage is then

multiplied by an arbitrarily chosen number (100 for the sake of simplicity). The resultant product is then subtracted from the original number, the difference is again multiplied by the replacement rate, and the subtraction is repeated. The number of times that this process must be repeated in order to reduce the original number to one-half its original magnitude is equal, in time units used, to the time required for one-half of the animals to be replaced, or simply to the median life expectancy.

Mean population size could be immediately computed from existing data. Replacement rates for the fished population were computed by assuming that the number of surviving newborn was equal to $\left(\frac{1-p}{p} \text{ times the mean yield}\right)$, where p is the percentage fishing.

No computation of median life expectancy was made for the unfished populations since not so great care was exercised in recovering all of the dead animals at censusing, making computation of the mean number of newborn less satisfactory than in the fished populations.

Calculated median life expectancies for all of the fished populations are listed in Table 5. It is clear that the median life expectancies of the animals that survive fishing in the highly fished populations are greater than those of the less highly fished populations, although the data do not permit more precise analysis of the relation between fishing and median life expectancy. The relation would be expected on the basis of previous analyses which indicate that life expectancy is increased by increasing the food supply per animal (Slobodkin 1954).

TABLE 5. *Median and mean life expectancy*

Population		% replacement per census	Median life expectancy, in days	Approx. mean life expectancy
L-19	25%	13.05	19.8	17.7
	50%	16.89	15.0	
	75%	10.83	24.2	
	90%	8.06	33.0	31.4
H-19	25%	12.40	21.0	17.8
	50%	9.14	29.0	
	75%	8.03	33.2	
	90%	7.43	36.0	34.6
H-15	25%	14.76	17.4	15.6
	50%	13.25	19.6	
	75%	10.78	24.4	
	90%	8.24	32.2	31.0

Mean life expectancy, the average age of animals at the time of their death, can only be computed when the shape of the survivorship curve is known (Deevey 1947). We have not conducted experiments to determine survivorship curves. Frank (1952) has published survivorship curves for *Daphnia pulicaria* maintained under constant "density" conditions. His experiments were discontinued before the last animals had died. It is still possible, nevertheless, to use his data to make some estimate of the relation between median and mean life expectancy in these experiments.

Since Frank's data are presented in terms of "density" it is first necessary to translate his density values into terms which are meaningful in the present context. Frank states that mean population size under conditions of constant feeding was equal to 8 animals per cc. Since we know that population size in unfished populations is directly proportional to food supply, we can assume that the physiological condition of animals in an unfished population is essentially the same as that in a group of *Daphnia* living under a density of 8 in Frank's terminology. We can further assume that as population size is reduced by fishing in these experiments the equivalent "density" will be proportionately reduced.

As will be explained below, there is some reason to believe that the estimates for mean size of the 25% fished populations are somewhat more authoritative than those for the unfished populations. Also, as shown in Figure 1 the difference in mean size to be expected between unfished and 25% fished populations in these experiments is small. We have therefore considered that Frank's density of 8 was equivalent to the mean density in 25% fished populations in these experiments.

The ratios of the mean size of the 90%

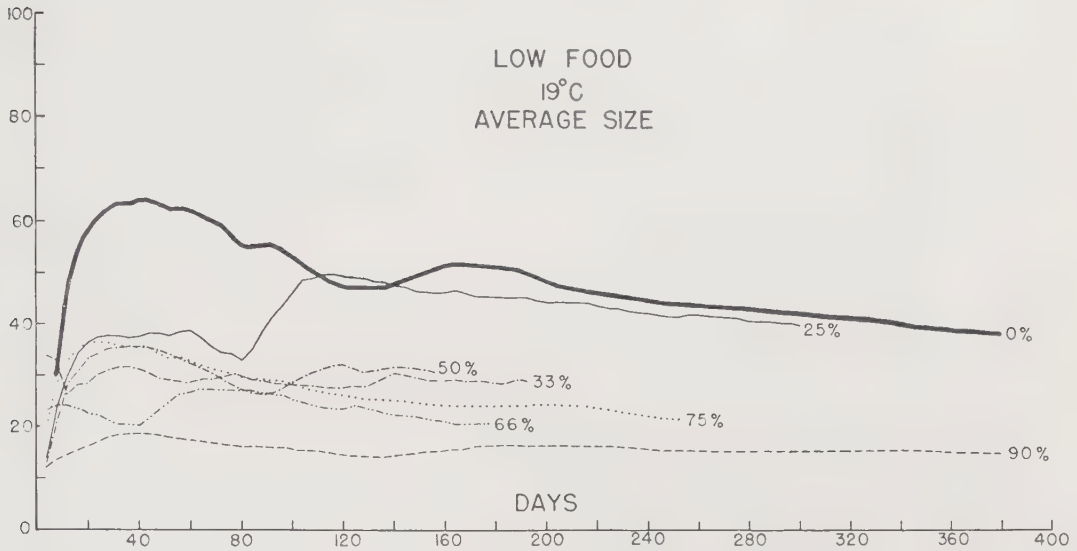

FIG. 14. Cumulative mean population size as a function of time in series L-19. Note the departure from a stable estimate of the mean in the populations fished at rates of 33%, 50%, and 66%.

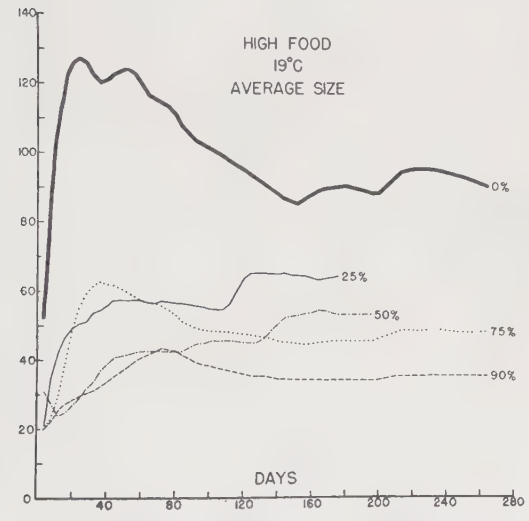

FIG. 15. Cumulative mean population size as a function of time in series H-19. Note that the estimate of mean population size in the unfished control was excessively high at the termination of the experiment.

fished populations of series H-19, H-15, and L-19 to the 25% fished mean population size are 1.805, 2.430, and 2.685 respectively. The average ratio is 2.31. Assuming the density equivalent of a 25% fished population to be 8, the mean density equivalent of a 90% fished population is 3.45.

Frank's experiments on survival were run at densities ranging from 9 to 1.5. No experiments were conducted at densities of 8 or 3.45. Frank's data were presented in units of median life expectancy. Considering the median life expectancy of population H-19 25% to be 21 days and graphically determining the mortality per day from Frank's published data for a density of 9, we can consider the mean life expectancy of population H-19 25% to be 17.8 days. Similarly, mean life expectancy acquired for the population H-19 90% (by graphically interpolating between Frank's survivorship curves at densities of 1.5 and 4.5 and extrapolating the terminal portions to zero survivors) is 34.6.

The weaknesses of the procedure are obvious. We nevertheless feel that the median life expectancy of *Daphnia pulicaria* populations is from 1.18 to 1.06 times the mean life expectancy. The overall effect on the shape of the survivorship curve of increasing population density was not very great over the density range considered.

The significance of mean values

Throughout our previous discussion we have been referring to mean values of various sorts derived from all of the data available about individual populations.

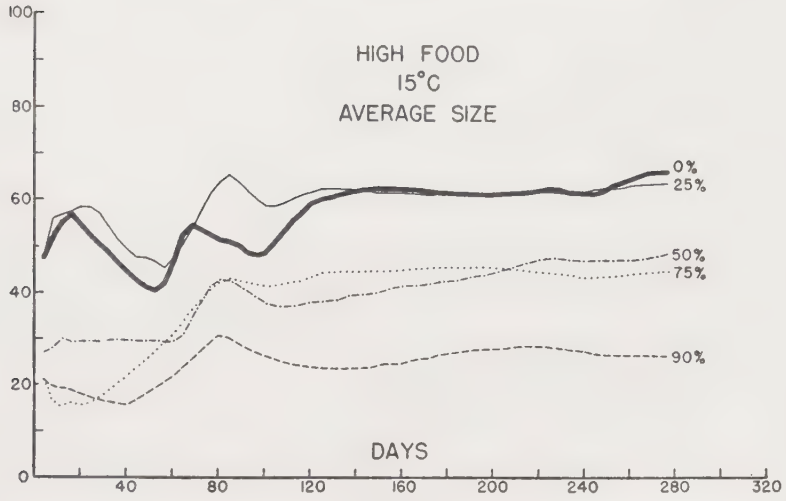

FIG. 16. Cumulative mean population size as a function of time in series H-15.

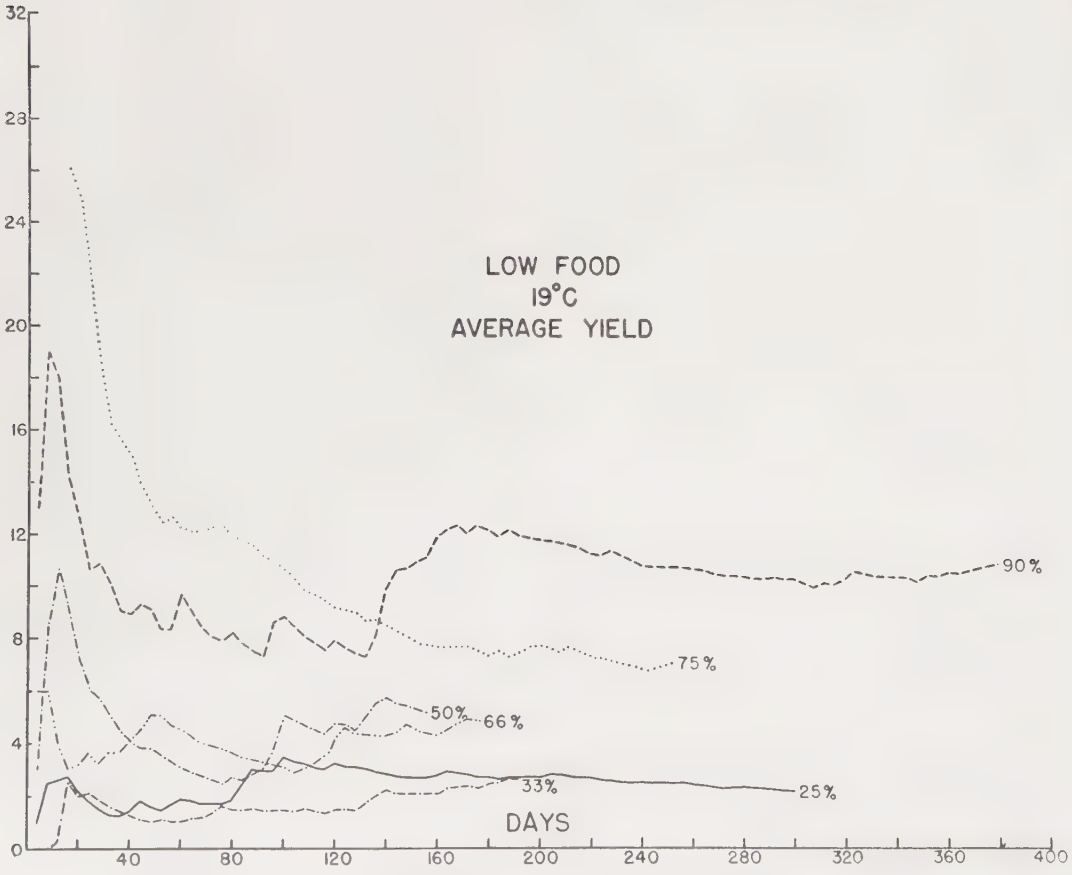

FIG. 17. Cumulative mean yield as a function of time in series L-19.

Since our populations are auto-correlated time series, the significance of these mean values cannot be determined by normal statistical techniques, which depend on the independence of successive estimates of the mean.

We must, nevertheless, have some objective criterion for determining the relative degree of confidence that can be placed in these means, or in general there must be some criterion for determining when all of the available information has been extracted from a given experimental population. If we consider any system which is fluctuating within certain bounds, the estimate of the mean state of that system over a given time interval will also tend to fluctuate. The shorter the period over which the mean is estimated the less reliance can be placed in it, and obviously the mean estimated over an effectively infinite length of time will not be altered by subsequent observations of the system. That is, if, for example, we plot the cumulative mean size for a population (for the time interval prior to any particular time) against time we will find the graph of the cumulative mean will fluctuate greatly at first, and then as time goes on, new observations will make relatively less difference to our estimate of the cumulative mean, and the graph of cumulative mean size against time will approximate a straight horizontal line. When this stage is reached, we can confidently discontinue the experi-

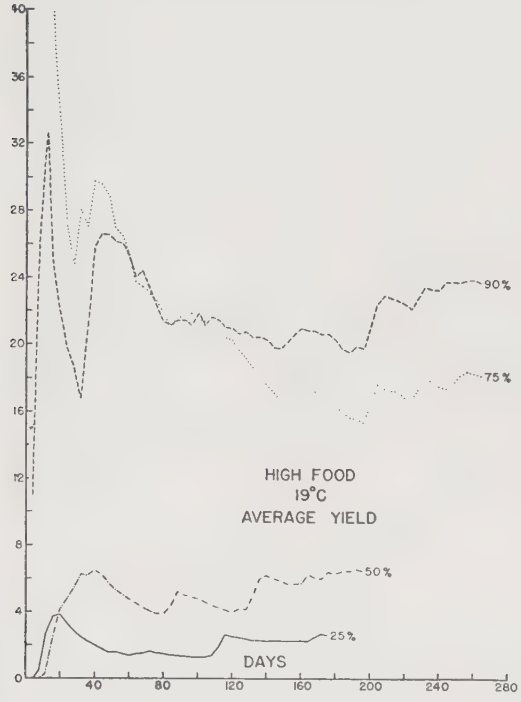

FIG. 18. Cumulative mean yield as a function of time in series H-19.

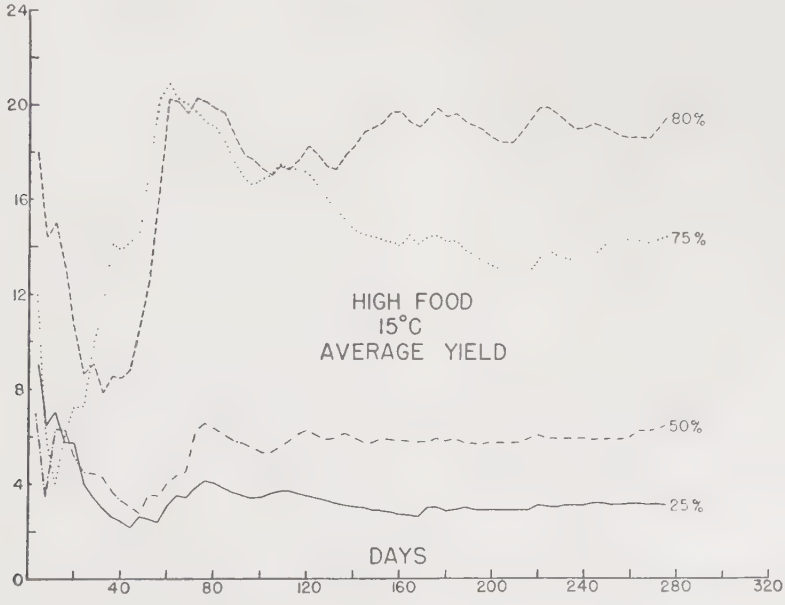

FIG. 19. Cumulative mean yield as a function of time in series H-15.

ments, on the assumption that all interesting information has already been acquired.

In Figures 14 to 16 cumulative mean population size has been plotted against time for all three experimental series. In general the terminal portions of these graphs are straight horizontal lines. In series H-19 the unfished population is not yet stabilized nor is the unfished population in series H-15, although the inadequacy of the size estimate is probably less in this case. There is an increasing trend of the estimate of the mean in series H-15 at 50% fishing and decreasing trends are apparent in series L-19 at 0 and 25% fishing. The estimates of the mean for the 33%, 50% and 66% fishing levels of series L-19 are weaker than the others.

In Figures 17 to 19 cumulative mean yields have been plotted against time for the three series. In general, yield estimates are more likely to be in error than population-size estimates but the error is probably not great enough to seriously distort the relation presented in Figure 1.

DISCUSSION

Many of the results of this investigation may be considered as suggestive but cannot, at the present time, be integrated into any general theory. Among these are the interaction between yield and fishing, population size and fishing, and the life expectancy effects. Some of the results, particularly the interactions between fishing and stability, are probably of more immediate theoretical significance. It should be borne in mind throughout that very few experimental exploitation studies have been attempted, so that comparative data are generally lacking.

Population size and yield

In the present experiments, yield per residual individual, increased in a non-linear way with fishing intensity while population size decreased non-linearly. It is apparent from elementary geometrical considerations that the product of two curves, one of which is increasing non-linearly and the other decreasing non-linearly, can be either a unimodal or bimodal curve, depending on the precise shape of the original curves. If the type of relation between fishing intensity, population size, and increase per individual found in our experiments is at all general, then bimodal yield versus fishing intensity relations may prove to be fairly common. The low-fishing-rate maximum in the yield versus fishing intensity relation would be due to a large number of animals, each increasing at a relatively low rate. The high-fishing-rate maximum would represent a small number of animals each reproducing or growing at a very rapid rate. The intermediate trough would be due to a fishing intensity which has lowered the population size enough to reduce the total yield, but not enough to permit compensatory increase in yield per individual. The precise pattern will depend on the mechanism of density interaction in the species involved.

Stability in populations and communities

Given any set of varying environmental factors, such as light, temperature, or the chemical composition of the air or water that surrounds the animals, different species will fluctuate to different degrees in population size. A two-day drought might destroy certain populations of insects completely but have no noticeable effect on a population of elephants in the same region. We will use the term "intrinsic variability" to refer to the relative degree of responsiveness of populations of different species to environmental variation. A species with a high intrinsic variability will show more fluctuation than a species with a low intrinsic variability when they are both subjected to identical environmental conditions.

The "actual variability" will be taken to mean the observable fluctuations in population size in a particular environment and is considered to equal the product of the intrinsic variability and the fluctuations of relevant environmental factors (including interaction with other species in the community). It seems intuitively clear that the overall actual variability that will be

found in a community of many species (defined in the sense of MacArthur 1955), will be some combination of the actual variabilities of the component species.

MacArthur (1955) has shown that the formal properties of the food web of a community will determine its intrinsic stability in part. In particular he has shown that, with a constant number of species in a community, the intrinsic stability of the community increases with the number of links in the food web. It is therefore clear that if we are going to determine the actual variability of a community as a combination of the variabilities of the component species we must take account of the food web and cannot simply sum the actual variabilities of the component species.

We have demonstrated that in our fishing experiments the total actual variability present in the population-predation system is unchanged by fishing rate. This means that the actual variability removed from the residual population in the form of yield variability is quantitatively transferred to the environmental variability (i.e. food supply) of the predator. A predator is, therefore, not only subjected to the variability of the physical environment, which will also affect its prey, but also to the actual yield variability inherent in the process of predation. We can therefore consider that the predators should either fluctuate to a greater degree than their prey or that the intrinsic variability of predators is in general less than that of animals lower in the food chain.

As a matter of fact, predatory species show relatively less actual variability than their prey. Therefore we conclude that the intrinsic variability of predatory species is relatively low.

This low intrinsic variability can be assigned to several causes. In general predators are larger and longer-lived than their prey. These properties tend to prevent small scale spatial and temporal irregularities from seriously influencing the predator populations.

Predators in general have a lower reproductive rate than their prey. Variability is decreased by this reduction in reproductive rate, presumably according to the pattern shown in Figure 11.

We can tentatively conclude that actual variability in a natural community is transmitted through the food chain in much the same way as energy. Each species in the community is offered a certain amount of environmental variability, either from the physical or biological environment. This variability may be amplified or reduced by that species as a function of its own intrinsic variability. Certain general observations on predators, which indicate that they have a low intrinsic variability, presumably associated with low thermodynamic efficiency in energy conversion (MacArthur 1955, Slobodkin 1953a) would seem to indicate a selective significance for community stability during the course of evolution, or equivalently a selective significance for population stability which has been of greatest effect on predator species. If predators, by and large, have lower intrinsic variability than their prey it becomes of interest to discover, if possible, the evolutionary conditions required for the development of low intrinsic variability. That is, is it conceivable that low variability as such might have a selective advantage? An animal characterized by low actual variability in population growth will have a lower rate of growth, lower reproductive rate, and lower thermodynamic efficiency in the conversion of food into protoplasm (Smith 1954). The interesting problem is how could an animal of this sort have a selective advantage over a more rapidly reproducing, more efficient animal of the same species. Lack (1954) has discussed the problem of the development of relatively low reproductive rates in populations of birds and small mammals and presents evidence which indicates that the survival of animals from large litters or broods is significantly lower than that of animals from smaller litters or brood. In effect, the large litters were too large to receive the amount of parental care per animal which would admit of optimal survival. He further notes that the clutch size of birds increases with latitude. He attributes this to the increased hours of daylight, permitting more time for

hunting of food by the parental birds. This viewpoint has been criticized by other authors (Skutch 1949) on the grounds that parental birds do not seem to exert undue effort in the care of their young and probably could care for a larger clutch if their activities were more clearly focused on care of the young. Ignoring this kind of objection and assuming that litter or clutch size is actually hereditary to some degree, which is supported by evidence from domestic animals presented by Lack (1954), Lack's argument is superficially a good one.

It can, however, be considered to be part of a broader argument, which for the moment rests on fairly speculative grounds, but nevertheless can be stated in some detail. The basic problem faced by Lack is the apparent inconsistency between the general tenets of modern evolutionary theory, which would predict that an animal with a high reproductive rate would have a selective advantage over a member of the same population with a lower reproductive rate, all other conditions being equal, and the observed reduction of reproductive rates during the course of evolution in certain species. Arguments to the effect that territoriality, parental care, courtship behaviour, etc. arose through evolution for the "good of the species" are justly condemned by Lack and most other modern investigators as vitalistic, orthogenetic, and generally out of line with the modern philosophical approach to biological problems. Several arguments have nevertheless been presented on sound theoretical and experimental grounds which permit the development of a non-vitalistic approach to the problem of group selection. These examples will be discussed in order of generality, and the relevance of the present studies to them will then be introduced.

Slobodkin (1953b) developed a hypothetical model in which a species was assumed to exist as a series of semi-isolated populations. Each one of these populations was assumed to be highly unstable, with a very high reproductive rate. It was further assumed that in the course of time each one of the semi-isolated populations would have become extinct, due to excessive population fluctuation, were it not for the arrival of migrants from the other semi-isolated populations which either recolonized the localities suitable for the species or damped the fluctuations to some degree. If a mutant which has a lower reproductive rate (hence higher population stability) should arise, it would be eliminated by natural selection in favor of the more efficient and less stable form. However, if the rate of migration between populations should now decrease, due to the development of barriers of some sort, the pattern of selective advantage would shift in favor of the less efficient, more stable form which was capable of persisting in one place without the arrival of new migrants. The conditions for the development of low reproductive rates, high complexity, low efficiency, and high population stability would be extreme isolation between colonies of the same species. Furthermore, unstable populations would be expected to have mechanisms for rapid migration, or a resting stage to permit temporal redistribution, or both. (These mechanisms are discussed further in Slobodkin 1954.) This basic argument permits further discussion of the evolution of population stabilizing factors without the omnipresent trap of vitalism.

On the basis of a simple mathematical analysis of the form of density dependence in various groups of species, Slobodkin (1953a) showed that a "social" species, defined as a species in which the density term in the population equation must be computed as a second or higher order function of the number of animals present, will come to equilibrium at a lower population size than a non-social species, and that the equilibrium value would be less dependent on alterations in the environment than it would be in a non-social species, all other factors being equal.

This is essentially a simplified form of the argument developed by Smith (1954). Smith noted that over any long period of time the average increase of any population is approximately zero. Nevertheless, the "intrinsic rate of natural increase" (Andrewartha and Birch 1954) differs widely from species to species. Smith considers that the

average "harshness" in some sense of the environment is proportional to the intrinsic rate of natural increase. That is, a species with a high intrinsic rate of natural increase is more often faced with the problem of rapidly taking advantage of an ecological opportunity than a species with a low intrinsic rate of natural increase. In our notation this would be a species with a high actual and intrinsic variability. Conversely, in the present experiments removal of the newborn has lowered the effective rate of increase and correspondingly reduced actual variability.

Furthermore, behavioral complexity in a species, including such things as intelligence and alertness, clearly require energy. Energy so utilized is no longer available for growth or reproduction. Reduction of the intrinsic rate of natural increase is compensated for by further development of other aspects of the animals, all of which tend toward higher population stability. In this connection it should be recorded that many of the more bizarre forms of animal behavior and the extremes of slow development and low reproductive rate are found in isolated island populations (for examples see Richdale 1952, Murphy 1936, Marshall 1954, Hutchinson 1954b, etc.).

Nicholson (1954a), discussing his experimental studies of predation in *Lucilia cuprina* says: "That the genetical compositions of populations of the same species do often vary considerably from place to place is now well known; but natural selection (which governs these compositions) could not possibly produce and preserve the precise adjustment [between populations and their environment . . .]. To do so, it would often be required to operate in reverse by selectively destroying any abnormally potent individuals which appeared; for the preservation of these at the expense of the previously normal individuals by the characteristic process of selection would lead to progressive and indefinite population growth, in the absence of some other mechanism with a compensatory influence." In other words, the population control mechanism itself is subject to natural selection.

All of these ideas are essentially equivalent to that of Lack if the stipulation is made that natural selection tends to favor the individuals with the greatest number of ultimate descendants, not simply the greatest number of offspring. The validity of this statement is tautological.

If it be conceded that reduction of reproductive rate increases population stability, then we can consider that Figure 11 indicates the rate at which this increase of stability occurs. The animals which we removed from the population can be interpreted as never having been born, from the standpoint of the remaining animals, although the energy used in their production is not available for further growth. In the case of the *Daphnia* populations, it has simply been lost, but in actual cases of evolutionary reduction of reproductive rates this energy would presumably be available for further behavioral or morphological complexity.

The interaction between environmental and population stability

It has been noted that the seasonal appearance of insects is correlated with the seasonal breeding of the birds that will utilize them as food. When the insects are late, the breeding season of the birds is late, etc. (Lack 1954). This suggests a possible interpretation of some of the data found in the present experiments. We have previously discussed the fact that the feeding capacity of *Daphnia pulicaria* increases approximately sevenfold from birth to maturity. In nature, *Daphnia* tend to be seasonally distributed, with the first young being born in the spring shortly before the initial vernal plankton bloom. In fact, it is not unreasonable to consider that the algal food supply available in a pond increases approximately tenfold between the time the first large group of *Daphnia* are born and the time at which they reach their adult feeding capacity. That is, the increase in feeding capacity with age, which tends to produce instability in the laboratory, will probably not produce a corresponding instability in nature since the natural environment may be expected to expand proportionately.

It becomes of extreme interest to discover whether this relation between the expected

variability in the natural environment and the inherent variability of the population size is at all general. Data are not abundant but certain examples are available. Members of the genus *Chydorus* are small bottom feeding cladocerans that produce no more than two eggs at a time. These eggs are very large relative to the size of the adults. If we assume that the *Chydorus* are limited by food supply in the same way as daphnias, then we must consider that the lag effect involved in their increased feeding capacity as they grow larger is of the order of one to two. It might also be expected that the seasonal variation in food supply at a mud-water interface would not be so extreme as that found in the open water. *Daphnia magna* is a common, very large daphnid found in extremely small temporary ponds, where very great food supply variability would be expected. The young of *Daphnia magna* are much smaller in relation to the adults than they are in *Daphnia pulicaria*. Accurate figures for the size of the newborn are not available for enough species to carry this discussion much further. It is presented as a possibility at the present time. The same relationship might explain in part the latitudinal differences in brood size found by Lack and would also explain the increase in clutch size of the European robin, *Erithacus rubecula*, and other birds found when passing from regions of oceanic climate to the central continental mass (Lack 1954), in terms of the greater seasonal variation to be expected in a continental climate as opposed to an oceanic climate.

A critical case for this hypothesis which has not yet been analyzed would involve a species in which there is either no parental care for the young, as in reptiles, or in which parental care is not confined to the natural parents, as in 'rafting' of ducklings. If these should prove to have the same latitudinal variation in clutch size as has been found in species with parental care, then Lack's hypothesis as stated must be considered incomplete.

Relation between the experiments of Nicholson and Watt and the present studies

Nicholson's studies (1954a, b) consisted of maintaining *Lucilia cuprina* in situations in which either the larvae or the adults were limited in food supply, and in situations in which oviposition by the adults was made more difficult by interposing a screen between the adults and the oviposition sites. In the normal population growth of *Lucilia*, extreme population fluctuations occur. These are due to the fact that a very small number of females is capable of laying enough eggs to thoroughly saturate the larval food supply. The larvae completely exhaust the food supply and then an overwhelming majority of them die. As the number of adult animals is decreased by fishing, with imposed destruction of as much as 99% of the emerging adult flies, the number of eggs laid is reduced sufficiently to greatly enhance the survival of the larvae, producing a compensatory increase in the pupal population. Situations in which the larval food was available in excess but in which the amount of protein food available to the adults was limiting were also highly resilient to the destruction of adults on emergence. Population oscillations were extreme in all but the situation in which 99% of the emerging adults were destroyed and larval food was limiting. In an experiment in which larval food was limiting and adult protein was also restricted, population fluctuations were damped without any imposed mortality. While the ecological differences between *Lucilia* and *Daphnia* make direct comparisons difficult, several of the differences between the experimental results are significant, in particular the extreme fishing intensity required to damp fluctuations in Nicholson's experiments. In a situation in which the population is limited by larval food supply, an emerging adult has already made its most significant contribution to population density at the time of removal, and its removal would not be expected to dampen population fluctuations. It seems likely that the elimination of population fluctuations at 99% removal is due to the extreme reduction in the reproductive potential of the population and has nothing to do with density time-lags dependent on growth rates. That is, sufficiently high destruction of the adults can alter the relative survival pattern so as to make

equilibrium possible. The relation between survival patterns, reproductive patterns, and the possibility of population equilibrium is discussed in Slobodkin (1955).

The interaction between yield and fishing intensity in Nicholson's study is almost identical with that reported in the present experiments, presumably because the main factor in the determination of yield was reproductive rate per individual rather than number of reproducing individuals in both studies.

The experiments of Watt (1955) were done on flour beetles and were designed in a somewhat more complex pattern than either Nicholson's studies or ours. Varying percentages of the larvae and adults were removed simultaneously at thirty-day intervals. In addition, experiments were conducted in which all the adults, all the pupae, and half the large larvae were removed at thirty-day intervals, the exploitation rate being calculated *a posteriori*. Each fishing level was replicated many times and the results are presented as averages of the replicates, making analysis of individual population variability impossible. The data are presented in the form of total standing crop only. So far as Watt's complex design admits of brief summarization, the rate at which animals entered any stage, i.e. adults, pupae, or larvae, was directly and simply a function of exploitation rate. Total variability was measured as distance between maximum and minimum productivity and total standing crop for thirty-day intervals. Measured in this way the variability of adult productivity increased with fishing intensity, but no other variabilities seemed to alter significantly with fishing rate. No tests of significance were applied to these relations by Watt, who has subjected his data to a detailed analysis using multidimensional matrices and has constructed a mathematical model using thirty-six parameters.

We must conclude that due to differences in experimental material and experimental design, translation and interpretation of the results of any one of the three experimental studies so far available in terms of any of the others is not particularly rewarding. The simple fact that all three situations demonstrate homeostasis in the response of populations to exploitation can be stated, but probably could have been stated *a priori*. It should also be emphasized that all three experiments contradict the simple exploitation models which have been based on the logistic curve, for the same reason that any experimental population of metazoa cannot be reconciled with the predictions of the logistic curve; that is, age structure and the variation of physiology with age are of overwhelming importance in the growth of populations of metazoa.

The experiments of Nicholson and Watt do not contradict the conclusions which have been drawn from the present experiments, but since the presentation of data in the three studies is not strictly comparable, they cannot be considered to confirm them either.

If this much variability and complexity can occur in the only three experimental exploitation studies which have as yet been completed, we must conclude that development of specific deterministic or stochastic models is premature. We can hope that future experiments will suggest new approaches and generalizations, but for the moment a general theory of exploitation seems further away than it did before the experiments were started. This in itself is probably a valuable conclusion to establish.

CONCLUSIONS

Removal of newborn animals at varying rates from populations of *Daphnia pulicaria* tends to reduce the size of the residual populations, but not in direct proportion to either the number or percentage of the newborn animals that have been removed. This lack of direct proportionality can be accounted for in terms of a shift in the age structure of the residual population, an increase in the growth rate and reproductive rate of those that survive the fishing procedure, and in their longevity. These effects can be adequately explained in terms of what is known of the dependence of *Daphnia* populations on the food supply per individual and the fact that removal of newborn individuals increases the available food supply for the animals that remain. Maximum yield occurred when approximately 90% of the newborn animals were removed.

As the removal rate increased, the absolute stability of the residual populations increased as did the stability per animal. The increased stability of the residual populations was precisely compensated for by increased variation in the yield from census to census. The variability of the total standing crop was unaltered by fishing.

The ratio of yield variability to population-size variability plotted against the percentage of the newborn that were not removed divided by the percentage of the newborn that were removed, produced an equilateral hyperbola with focus at the point 1,1. The simplicity of this relation makes us suspect that it is not confined to *Daphnia pulicaria* alone.

Two general conclusions that are indicated but not unequivocally demonstrated by the present study are that the observed low variability of populations of predators can be fitted into a general scheme of community stability patterns and that it seems very likely that the positive feedbacks in any population are adjusted to the expected variability in the environment of that population in nature, so that a highly variable system in the laboratory may not depart from equilibrium with the environment in nature.

Comparing these studies with other published experimental work on fishing laboratory populations, it was found that differences in the published results to date only emphasize the diversity to be expected in an exploitation system and accentuate the need for further experimentation as a prerequisite for general theory development.

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